

GEOGRAPHIC VARIATION AND SYSTEMATIC STATUS OF MEXICAN LYRE SNAKES OF THE *TRIMORPHODON TAU* GROUP (COLUBRIDAE)

By ROY W. McDIARMID¹ AND NORMAN J. SCOTT, JR.²

ABSTRACT: Geographic variation in lepidosis and color pattern was studied in the nominal species *Trimorphodon collaris*, *fasciolata*, *forbesi*, *latifascia*, *tau*, and *upsilon*. Specimens were grouped into seven geographically separated samples which were then compared. Ranges of most characteristics overlap broadly; others vary independently and discordantly. Ventral-subcaudal scales decrease from north to south. Snakes from the Balsas-Tepalcatepec Basin have fewer dorsal bands than do snakes from other areas. They also have a relatively uniform head pattern. Specimens from other areas have a complex head pattern consisting of prefrontal bars, interocular bars, and discrete parietal marks in various combinations. Head pattern and body band analyses indicate limited genetic exchange between the Balsas-Tepalcatepec Basin samples and those from other areas, apparently the result of secondary contact in southern Jalisco and adjacent Michoacán. The Transverse Volcanic Range and the Sierra Madre del Sur apparently are effective in restricting genetic exchange.

The above nominal species are assigned to the synonymy of *Trimorphodon tau*. *Trimorphodon tau tau* is maintained for the foothills and plateau populations and *T. tau latifascia* (new combination) is assigned to the Balsas-Tepalcatepec Basin populations. *Trimorphodon tau* is redescribed and its distribution delimited. Character variation in a brood from Puebla approaches the variation typical of the entire Puebla sample.

INTRODUCTION

In the years following 1935, rather extensive collections of amphibians and reptiles were made in México. Early reports on many of these collections, culminating in the Mexican checklists by Hobart M. Smith and Edward H. Taylor (1945, 1948, 1950), are extremely useful in elucidating the distribution and relationships of the many components of this complex herpetofauna. During the past 15 years, reports on collections from various parts of México have continued to appear. Unfortunately, some of these reports have confused rather than clarified our knowledge of the distributions and systematics of certain of the Mexican species (see Duellman, 1966, for additional discussion). An example of such confusion is found within the snake genus *Trimorphodon*.

¹Research Associate in Herpetology, Los Angeles County Museum of Natural History and Collegiate Division of Biology, University of Chicago. (Current address: Dept. of Zoology, University of South Florida, Tampa.)

²Biological Sciences Group, University of Connecticut.

All 12 nominal species of *Trimorphodon* have been reported from México (Smith and Taylor, 1945). Smith (1941) divided the genus into two apparently natural groups. The *biscutatus* group, characterized by large chevron-shaped marks on the neck and head, included five nominal species (*biscutatus*, *lambda*, *lyrophanes*, *paucimaculatus* and *vandenburghi*) that range generally from the southwestern United States southward through the Pacific lowlands to Costa Rica. The *tau* group, characterized by a light, transverse nuchal collar of varying width, included seven nominal species (*collaris*, *fasciolata*, *latifascia*, *tau*, *upsilon* and *vilkinsonii*) whose ranges encompass upland and mountainous portions of southeastern New Mexico, southwestern Texas and México, north of the Isthmus of Tehuantepec.

We became interested in the *Trimorphodon tau* species group in the course of an extensive study of the herpetofauna of Sinaloa, México (Hardy and McDiarmid, 1969). In attempting to allocate specimens, we realized the need for a revision of this group of snakes and so began a study of the geographic variation and systematic relationships among the described forms, with emphasis on the zoogeographic implications of the distribution of specific characteristics.

HISTORICAL REVIEW

Cope (1869) described *Trimorphodon tau* from a single specimen collected by Sumichrast, supposedly from the western part of the Isthmus of Tehuantepec, and *Trimorphodon upsilon* from a specimen collected in Guadaluajara, México by Major (see Zweifel, 1959 for discussion of this collection).

Later in the same year, Peters (1869) described *Dipsas biscutata* var. *latifascia* from specimens collected in Puebla by Berkenbusch.

These descriptions were the first for representatives of the *tau* species group, though specimens of these species were known previously. Jan (1863) listed four specimens of *Eteirodipsas biscutata*, one from Méxio. Nine years later this same specimen was illustrated in Jan and Sordelli (1872) and listed as part of the collection of "Westphal-Castelnau a Montepellier." The Mexican specimen definitely is not *Trimorphodon biscutatus* (Duméril, Bibron and Duméril, 1854), nor is it representative of a species of the *biscutatus* group as presently understood. In fact the color pattern, especially of the head (Jan and Sordelli, 1872: vol. 3, livr. 39, pl. 1, no. 3), is similar to the pattern of the holotype of Cope's *Trimorphodon upsilon*.

Cope (1875) described a fourth species of the *tau* group, *Trimorphodon collaris*. This specimen, also collected by Sumichrast, was from Orizaba, Veracruz. In 1882 Sumichrast pointed out that the type specimen of *Trimorphodon tau* was collected near Quiotepec, between Tehuacán and Oaxaca and was not from the western part of the Isthmus of Tehuantepec as stated by Cope (1869) in the original description. In this same publication, Sumichrast (1882) listed "los individuos típicos" of *Trimorphodon collaris* from Tuxpango, near

Orizaba, Veracruz. However, in the description of *T. collaris* Cope (1875) made no reference to specimens other than the type. The location of any additional specimens of *T. collaris* collected by Sumichrast is unknown.

Günther (1895) pointed out the similarities between *Trimorphodon tau*, *collaris* and *upsilon*, and referred his specimens to *T. upsilon*. Günther considered Peters' *latifascia* synonymous with *Trimorphodon biscutatus*. Boulenger (1896) recognized *Trimorphodon tau* and *T. upsilon* as distinct species. Boulenger followed Günther's suggestion and included *Trimorphodon collaris*, as well as *Trimorphodon biscutatus latifascia* (Peters), in the synonymy of *Trimorphodon upsilon*.

Taylor (1939) reviewed Mexican species of *Trimorphodon* and revived Peters' name *latifascia* for specimens from Puebla and Morelos. Taylor recognized *T. upsilon* and *T. tau* as distinct species but considered *T. collaris* synonymous with *T. latifascia*.

In 1941 Smith surveyed the genus *Trimorphodon* and established the two species groups. He considered *Trimorphodon latifascia*, *T. upsilon*, *T. tau* and *T. collaris* distinct species. In addition Smith (1941) described two more forms in the *tau* group: *Trimorphodon fasciolata* from Tzaráracua Falls, Michoacán (one specimen) and *Trimorphodon forbesi* from San Diego, Puebla (one specimen).

After examining specimens of *Trimorphodon* from Michoacán, Schmidt and Shannon (1947) suggested that *T. fasciolata* might be conspecific with *T. latifascia*. Davis and Smith (1953) and Peters (1954) demonstrated that these two forms probably were representative of a single species.

Smith and Darling (1952) examined some specimens from Tamaulipas and San Luis Potosí and regarded *Trimorphodon upsilon* as a subspecies of *Trimorphodon tau*. Martin (1958) confirmed the conspecificity of these forms.

Duellman (1961) concluded that data were inadequate to support the retention of *upsilon* as a subspecies of *Trimorphodon tau*. He regarded *Trimorphodon tau* as a monotypic species that has a highly variable color pattern. Thus, if the systematic changes since Smith's revision (1941) are accepted, there are currently four species in the *tau* group, *Trimorphodon tau*, *collaris*, *forbesi* and *latifascia*.

Jones and Findley (1963) suggested that *T. wilkinsoni* might be related to *T. lambda*, a member of the *biscutatus* group.

METHODS AND MATERIALS

We have examined all known specimens, including holotypes, of the following nominal species of the *Trimorphodon tau* group: *tau*, *upsilon*, *collaris*, *latifascia*, *fasciolata* and *forbesi*. Locality, sex (determined by dissection), and the following features were recorded for each of the 197 specimens: number of ventral scales (counted according to the method outlined by Dowling, 1951), number of subcaudal scales including the tail tip, total number of

ventral and subcaudal scales, nature of the anal plate (divided or entire), number of supralabials, supralabials that contact eye, number of infralabials, the infralabial that is first separated from the chin shields by small gular scales, number of loreal scales (all scales between the preocular and nasal scales), number of preocular and postocular scales, and the number of primary and secondary temporal scales. The dorsal scale rows were counted one head length behind the parietal scales, at midbody and one head length in front of the anus. The number of scales in the light collar counted on the midline was recorded, as was the number of body and tail bands or blotches. The first cross band that showed any indication of splitting (the presence of a light center on the midline) was recorded. For each band-interspace-band sequence the number of scales on the midline was counted beginning with the first dark band-light interspace-second dark band, for the seventh dark band-light interspace-

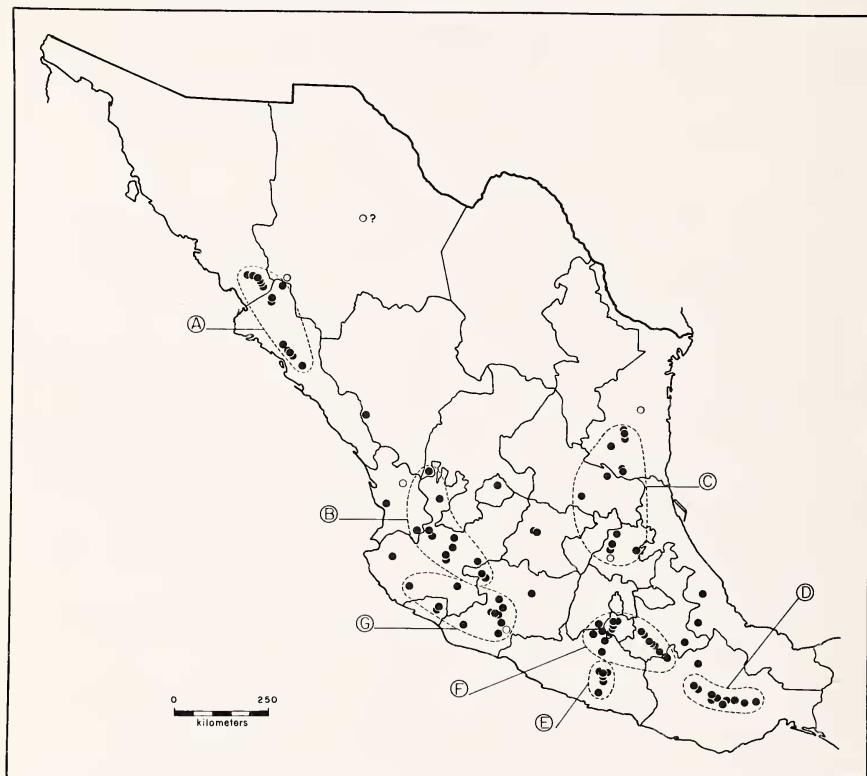


Figure 1. Distribution of *Trimorphodon tau* in México. Each dot represents a locality or localities of one or more specimens. Solid dots indicate specimens examined; circles indicate additional specimens or literature records. Samples analyzed are lettered A through G.

eight dark band, and at equivalent intervals along the body of the snake. In all instances the band-interspace-band sequence immediately anterior to the vent was counted. Detailed drawings of the dorsal head pattern were made for each specimen.

Specimen localities were plotted on a topographical map of México and grouped into seven geographical units (Fig. 1). These seven samples, hereafter referred to as populations A through G, include specimens from the following areas:

Population A (25 specimens)—from localities in the foothills of the Sierra Madre Occidental of southern Sonora and northern Sinaloa. These localities are separated from population B to the south by nearly 480 kilometers.

Population B (15 specimens)—from localities in the upper drainage of the Río Santiago and its tributaries in Nayarit and Zacatecas and from the general vicinity of Guadalajara and Lago de Chapala in Jalisco and adjacent Michoacán. These snakes probably are continuously distributed in suitable habitats northward through Sinaloa, as indicated by two specimens from western Durango, but are separated into two populations, A and B, because of the lack of adequate material from the intervening area.

Population C (14 specimens)—from localities in Tamaulipas, San Luis Protosí and Hidalgo in the eastern drainage systems of the Río Pánuco and Río Tamesi. There are six specimens known from within the 400 kilometer hiatus that separates population C from population B, the latter of which is restricted to western drainages.

Population D (20 specimens)—from localities in central Oaxaca. This sample is situated about 480 kilometers southeast of population C with only a few specimens known from the intervening area. The uplifted southern section of the Mexican Plateau effectively separates populations C and D.

Population E (51 specimens)—a large sample from the vicinity of Chilpancingo, Guerrero located in the central part of the Sierra Madre del Sur. These localities are isolated from sample D by the eastern extension of the Sierra Madre del Sur and the mountains in northwestern Oaxaca.

Population F (25 specimens)—from areas in northeastern Guerrero and adjacent México and Morelos and from southwestern Puebla. These localities are in areas drained by the northeastern tributaries and headwaters of the Río Balsas. Population F is separated from E by the arid Balsas Basin and from D by the mountainous areas of northwestern Oaxaca. Population F is separated from sample C south of the volcanic peaks and high southern portions of the Mexican Plateau.

Population G (19 specimens)—from parts of Colima, southern Jalisco and western Michoacán. These localities are situated in areas drained by the Río Armería and Río Coahuayana (Autlán and Contla, Jalisco and Colima) or by the major northwestern tributary of the Río Balsas, the Río Tepalcatepec (Michoacán). This sample is isolated to the northwest of E by the arid Balsas

Basin and to the south of B by the Transverse Volcanic Range and western portions of the Mexican Plateau.

Specimens removed from the geographic range or topographically isolated from these units were considered separately. In other words, we did not extend the geographical coverage of our units to accommodate individual specimens.

After the seven groups were established, the meristic, scale and pattern characteristics were compared within each unit and among the seven units.

GEOGRAPHICAL VARIATION

LEPIDOSIS

Ventral and subcaudal scales.—Ventral scales vary from 20-231 in males and from 210-243 in females. Subcaudal scales range from 61-85 in males and from 55-80 in females. Females average 2-11 more ventrals than males in the various populations. However, males on the average possess 8-11 more subcaudals than do females in the same population. The relatively shorter body and longer tail of males, as indicated by fewer ventrals and more subcaudals, apparently is the result of their more anteriorly placed cloacal opening. This condition is probably an accommodation for the relatively long hemipenes in the tail. The converse probably is true of females which have a longer, more bulky body to accommodate eggs (Klauber, 1956:167).

The number of ventral and subcaudal scales in snakes is indicative of the number of vertebral segments (Dowling, 1951:99). To test the assumption that there is little or no sexual dimorphism in the total number of vertebral elements in members of the same geographic population, we analyzed the number of ventral plus subcaudal scales for males and females in each of the seven samples using the Student's *t*-test. No significant differences (95 percent level) were found. Therefore, for purposes of analysis, we combined the ventral and subcaudal counts of males and females in each population.

The ventral-subcaudal scales range from 265-319. The higher numbers are characteristic of the northwestern population in Sonora and Sinaloa and the lower numbers are from the southern population in Oaxaca. Variation in numbers of ventral-subcaudal scales in the seven populations is illustrated (Fig. 2). The relative geographic positions of specimens from localities outside of the geographic limits of the prescribed populations are plotted by number in Figure 2.

There is a north to south reduction in the number of ventral-subcaudal scales within population A. The specimens from southern Sonora have 298-319, $\bar{x} = 307$ ($N=11$). Specimens from the Río Fuerte in northern Sinaloa have 300-306, $\bar{x} = 303$ ($N=4$). Specimens from north central Sinaloa have 293-308, $\bar{x} = 303$ ($N=10$). Two specimens from Ventanas, Durango (300 and 302 scales), and a specimen from the vicinity of San Blas, Nayarit (294 scales) are the only known specimens from the 480 kilometer distance between

populations A and B (Fig. 2, Nos. 1-3). Their counts are intermediate and suggest that additional material from the intervening area would show that the north to south reduction in the number of ventral-subcaudal scales exhibited in population A continues into B. A specimen from La Cumbre, Jalisco (Fig. 2, No. 4) has 292 ventral-subcaudal scales.

Within population B, three high counts (299, 299, 303) are characteristic of specimens from northwestern localities of population B, at Barranquitas, Nayarit, and near Magdalena and Bolaños, Jalisco, respectively. Two specimens from the southeastern parts of population B near Emiliano Zapata, Michoacán have low counts (282, 287).

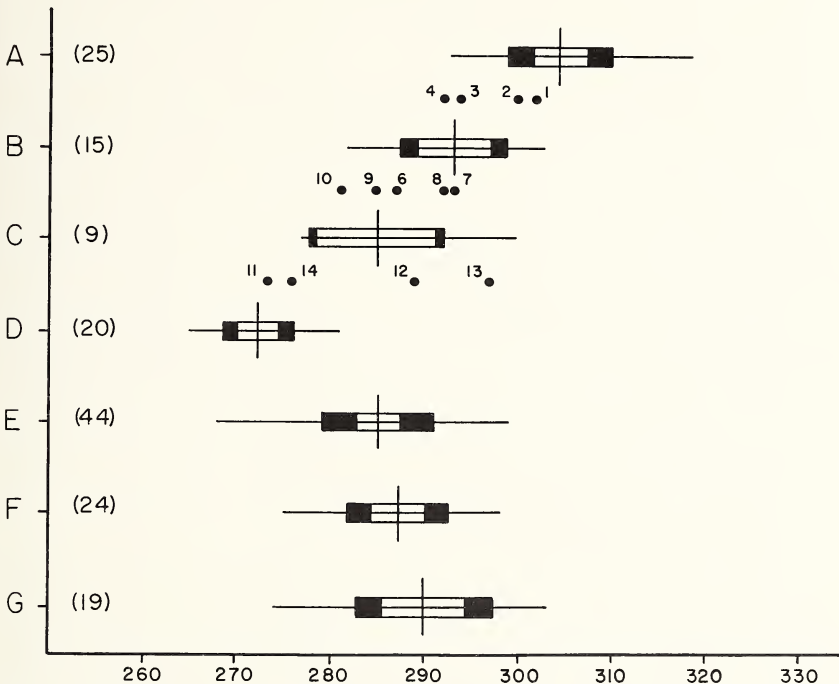


Figure 2. Statistical analysis of the number of ventral plus subcaudal scales in populations A through G of *Trimorphodon tau*. The number in parenthesis indicates sample size of each population. The horizontal lines indicate sample range and the vertical lines sample mean. The black rectangles represent one standard deviation on each side of the mean; the white rectangles represent 2.646 standard errors on each side of the mean (Eberhardt, 1968). Dots represent specimens from the following intermediate localities outside the geographic range of the samples: 1, 2, Ventanas, Durango; 3, N of San Blas, Nayarit; 4, La Cumbre de los Arrastrados, Jalisco; 5, 7 mi S Rincón de Romos, Aguascalientes; 6, 7, Tacicuaró, Michoacán; 8, 10, Guanajuato, Guanajuato; 9, Mt. Cubilete, Guanajuato; 11, Jalapa, Veracruz; 12, Tuxpango, Veracruz; 13, San Diego, Puebla; 14, Quiotepec, Oaxaca.

Specimens from population C in eastern México have fewer ventral-subcaudal scales than specimens from B and in this character indicate a continuation of a cline. The trend is continued within population C in that northern specimens have higher totals than do southern specimens. The highest counts (290, 300) are found in northern specimens from Tamaulipas, while the lowest counts (278, 277) are from snakes from more southern localities in San Luis Potosí and Hidalgo.

Two specimens from Tacícuaro, Michoacán on the interior drainage of the Río Grande de Morelia and three from the vicinity of Guanajuato, Guanajuato in the drainage of the Río Lerma are situated between populations B and C. Four of these five specimens exhibit ventral-subcaudal counts that lie on or between the means for populations B and C, and thus reflect their intermediate geographic position (Fig. 2, Nos. 6-10).

Specimens from population D have the lowest ventral-subcaudal counts and are from localities at the southern limit of the range. Most of these localities lie within the Pacific drainage of the Río Verde although some are from localities in the Atlantic drainage of the Río Papaloapan. These eastern specimens, when considered together with two other specimens from eastern localities north of population D (Fig. 2, Nos. 11, 14), suggest a possible connection between samples C and D along the eastern edge of the Mexican Plateau. The specimen from Jalapa, Veracruz (Fig. 2, No. 11) and the type of *Trimorphodon tau* from Quiotepec, Oaxaca (Fig. 2, No. 14) have ventral-subcaudal counts that are within the range of variation of population D but slightly higher than the average and thus approach populations C and F in this character.

Snakes from the largest sample, population E, average about 13 more ventral-subcaudal scales than specimens in population D and, in this respect, are nearly identical to those in population C (Fig. 2). Sample C is located nearly 400 kilometers north of E and separated from it by the Balsas Basin and the Mexican Plateau.

Population F averages slightly more ventral-subcaudal scales than E, but this difference is not significant at the 95 percent level. All known specimens in sample F are from localities in the upper Balsas Basin. The holotype of *Trimorphodon collaris* from western Veracruz (Fig. 2, No. 12) and the holotype of *T. forbesi* from southern Puebla (Fig. 2, No. 13) are both from localities in eastern drainage systems. These two specimens have ventral-subcaudal counts similar to those of population F. Thus, specimens from southeastern Puebla and adjacent Oaxaca and from Veracruz have two patterns in the number of ventral-subcaudal counts. The holotypes of *Trimorphodon collaris* and *T. forbesi* (Fig. 2, Nos. 12, 13) are more similar to specimens from population F, while the holotype of *T. tau* and the Jalapa specimen (Fig. 2, Nos. 11, 14) are more similar to snakes from population D.

Snakes from population G have more ventral-subcaudal scales than are found in either E or F. In this respect sample G approaches sample B which

lies immediately to the north. There is no significant difference (95 percent level) between samples B and G in the numbers of ventral-subcaudal scales.

This analysis shows that there is a clinal trend in total ventral-subcaudal scales within population A and among populations A, B, C and D, with higher counts in the north and lower counts in the south. Populations E, F, and G are more closely related to each other than they are to either of the two geographically adjacent populations, B in the north and D in the south. However, these three Balsas-Tepalcatepec Basin samples (E, F, G) have the same trend of higher totals in the north and lower totals in the south. In this instance, however, the trend is somewhat less marked.

Anal scale.—The anal scale is divided in all specimens except one. A male from Morelos (TCWC 7390) has an entire anal scale.

Loreal scales.—The number of loreal scales varies from two to five on each side of the head, with the majority of specimens having either two or three loreal scales (Table 1). Two loreals are more common in specimens from populations B, C and D, while three loreals are typical of populations A, E, F and G.

Preocular scales.—Although preocular scales may vary in number from one to four, the majority of snakes in all populations have three (Table 1). Specimens with two preocular scales are found in all populations except D. A single preocular is present in one specimen from population F.

Postocular scales.—Three postocular scales are characteristic of most specimens (Table 1). All snakes from sample F have three postoculars. Two postocular scales occasionally occur in the other six samples. Four scales are known only from specimens in populations A and E.

Temporal scales.—Most specimens have either two or three primary temporals and three or four secondary temporals. The majority of specimens in populations A, E, F and G have three primary and four secondary temporal scales, while specimens from population B, C, and D usually have two primary and three secondary temporals (Table 1). The differences may reflect the smaller sample sizes of these populations. A single primary temporal occurs only once, in population B; five primary temporals occur only once, in population E. In five instances snakes from sample D have two secondary temporals.

A comparison of the total number of lateral head scales (loreal, ocular and temporal) for the specimens from each sample shows that the higher numbers and means are characteristic of populations A (28-37, $\bar{x}$ = 30.9, N=23), E (26-39, $\bar{x}$ = 30.8, N = 48) and F (26-34, $\bar{x}$ = 31.2, N = 25), while the lower totals and means are found in samples B (23-31, $\bar{x}$ = 28.2, N=14), C (25-31, $\bar{x}$ = 27.9, N=12) and D (24-32, $\bar{x}$ = 28.2, N=20). Population G (24-32, $\bar{x}$ = 29.0, N=19) is somewhat intermediate in total head scales but is slightly closer to the lower than to the higher values. There is considerable variation in the number of head scales within some populations and some variation among several populations. We do not consider the different head

scale characteristics to be of systematic importance in distinguishing any of the samples.

Labial scales.—Most snakes have either eight or nine supralabials, except in population C where all specimens have eight (Table 1). Eight is the more common number of supralabials in all populations except F, in which nine occurs more frequently. Only in sample D are specimens with seven supralabials found. The type specimen of *Trimorphodon tau* has six supralabials on each side, the lowest number known.

Although the fourth and fifth supralabials border the eye in the majority of specimens examined, some variation was noted. In populations A, D, E, and F occasional individuals have the fifth and sixth supralabial bordering the eye. One specimen from each of populations F and G has the third, fourth and fifth supralabials bordering the eye on one side while the fourth and fifth border the eye on the other. The fifth supralabial borders the eye on one side in two specimens from population F; the usual condition is found on the other side.

There is considerable variation in the number of infralabials from population to population and within populations (Table 1). Twelve is the most common number, although ten, eleven, and thirteen infralabials are found in nearly all samples. Population D has the lowest recorded number of infralabials (nine) and has a lower mean than do the other six samples.

The small gular scales usually separate the infralabial series from the chin shields at the level of the fifth or sixth infralabial scale. In population A this separation occurs in the majority of snakes at infralabial six. In population D this separation occurs in most specimens at infralabial five. In the other five populations the separation occurs about equally at the fifth or sixth infralabial. Occasionally the infralabial series may be separated from the chin shields at a level as far anterior as the fourth infralabial or as far posterior as the seventh.

Dorsal scales.—The dorsal scales of *Trimorphodon* are smooth, with paired apical pits. The scales are arranged in diagonal rows and vary considerably in number. The anterior count at one head length behind the head ranges from 21-27 rows; 75 percent of the individuals have 22, 23, or 24 rows. The number of scale rows at midbody varies from 17-25; 80 percent of the snakes have 22 or 23 rows. At one head length in front of the vent, there are between 14 and 18 rows, and at this level 83.33 percent of the sample have 15 or 16 rows.

The reduction in scale rows is similar to the reduction found in *Leptodeira* (Duellman, 1958:20). The reduction involves changes in the paravertebral row. The level (ventral scale) at which reduction in scale rows take place is highly variable with no geographic consistency.

PATTERN AND COLORATION

Cross bands.—The number of dorsal body bands (body and tail blotches) in individuals with complete tails ranges from 18-46, though evidence suggests

TABLE 1.

Range and Percent Distribution of Various Head Scales in
the Seven Populations of *Trimorphodon*

		A	B	C	D	E	F	G
No. of specimens		23	15	14	20	51	25	19
	2	6.5%	66.6%	75.0%	60.0%	18.0%	12.0%	44.7%
	3	87.0	33.4	25.0	35.0	79.0	86.0	55.3
Loreals	4	6.5	—	—	5.0	2.0	2.0	—
	5	—	—	—	—	1.0	—	—
	1	—	—	—	—	—	2.0	—
	2	6.5	13.3	14.3	—	8.9	2.0	15.8
Preoculars	3	93.5	83.3	85.7	97.5	88.1	90.0	84.2
	4	—	3.4	—	2.5	3.0	6.0	—
Postoculars	2	19.2	3.5	10.7	7.5	1.9	—	10.5
	3	76.6	96.5	89.3	92.5	94.1	100.0	89.5
	4	4.2	—	—	—	4.0	—	—
	1	—	3.5	—	—	—	—	—
	2	19.6	55.2	39.3	60.0	23.5	24.0	31.6
Primary	3	78.3	41.3	57.2	37.5	71.6	74.0	68.4
Temporals	4	21.0	—	3.5	2.5	4.0	2.0	—
	5	—	—	—	—	0.9	—	—
	2	—	—	—	12.5	—	—	—
Secondary	3	26.1	44.8	63.0	50.0	25.7	12.0	47.4
Temporals	4	60.9	55.2	37.0	35.0	72.3	86.0	52.6
	5	13.0	—	—	2.5	2.0	2.0	—
	7	—	—	—	10.0	—	—	—
	8	60.9	69.0	100.0	72.5	63.9	39.5	57.9
Supralabials	9	37.0	31.0	—	15.0	29.9	58.1	39.5
	10	2.1	—	—	2.5	6.2	2.4	2.6
	9	—	—	—	2.5	—	—	—
	10	2.1	3.3	9.5	27.5	2.1	4.6	—
	11	28.4	30.0	28.6	50.0	14.9	23.3	26.5
Infralabials	12	47.8	43.4	47.6	20.0	45.8	44.2	44.1
	13	21.7	20.0	14.3	—	35.1	25.6	20.6
	14	—	3.3	—	—	2.1	2.3	8.8

that higher numbers do occur (see below). The higher values are found in samples A, B, C and D while the lower numbers are characteristic of the three Balsas-Tepalcatepec Basin populations, E, F and G. The numbers of body bands for the seven populations and for geographically intermediate specimens are shown in Figure 3.

There is a decrease of dorsal body bands within population A from north to south. Specimens from Sonora have 27-36, $\bar{x} = 32$ ($N=11$); specimens from northern Sinaloa have 29-33, $\bar{x} = 30$ ($N=14$); specimens from central Sinaloa have 25-31, $\bar{x} = 28$ ($N=10$). Snakes from population B on the average have more body bands than specimens from population A, and snakes of population C tend to have more bands than those from B. Specimens that are geographically intermediate between samples A and B have an intermediate number of bands. The same is true for two specimens from the area between samples B and C (Fig. 3, Nos. 8, 9).

In population C the Hidalgo specimens apparently have more bands than

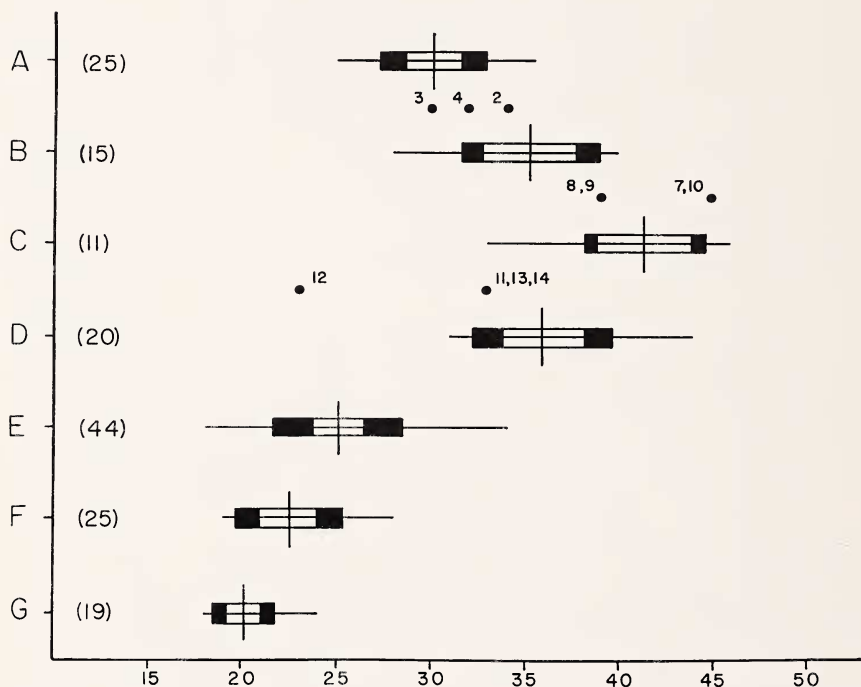


Figure 3. Statistical analysis of the number of cross bands in populations A through G of *Trimorphodon tau*. See legend to Figure 2 for explanation of diagrams and symbols.

do the Tamaulipas specimens. The only Hidalgo specimen with a complete tail has 43 body bands. Three other snakes from Hidalgo appear to have 40, 42 and 49 bands or more. These three specimens have damaged tails and, for this reason, are not included in Figure 3. The higher number of bands indicated for southern specimens in population C may account for the high numbers found in two of the intermediate specimens between B and C (Fig. 3, Nos. 7, 10). Both of these specimens (FMNH 105193, USNM 11370) are from localities slightly farther south than most of the localities in either B or C.

Specimens from population D, like population B, have fewer dorsal blotches than those from population C. Three of the four snakes from localities intermediate between C and D in eastern México are more similar to D than to C. The fourth snake (Fig. 3, No. 12), the holotype of *Trimorphodon collaris*, is much closer in band number to specimens from sample F.

Snakes from populations E and F average 11 to 13 fewer blotches than specimens from population D, the sample that is closest geographically. They are most similar to snakes from population A which is the farthest removed geographically. In band count, samples E and F are most similar to sample G. These populations (E, F, G) are significantly different from all of the other populations. Although populations B and G are in close geographic proximity, there is no overlap in the number of body bands. In fact these two samples are separated by a mean difference of 15 dorsal body bands.

The lengths of the bands may vary considerably on a single individual and among individuals of the same or different populations. In order to evaluate the differences in band size, the lengths on the middorsal scale row (as indicated by the number of included scales) of three band-interspace-band sequences were compared. The first sequence behind the collar (anterior), a mid-body sequence, and the last sequence before the vent (posterior) were used. These values are presented in Table 2.

In all populations the first dark cross band usually is the longest. The second cross band is longer on the average than either of the midbody bands, and they, in turn, always average longer than the posterior body bands. The mean band length of specimens from population A is greater than that of specimens from B, and mean band length in B is greater than in C (Table 2). In all instances the bands on snakes from population D average longer than bands in C but are shorter than bands on snakes in B.

Bands of specimens from populations E, F and G average longer than those of any of the other four samples. The only exception is the mean first band length of sample A which is longer than in sample E but never as long as in samples F or G. In general, specimens from population G have longer bands than specimens from F, and specimens from F have longer bands than specimens from E. The longest mean band lengths at all three body positions are characteristic of specimens from population G while the shortest band lengths are always found in population C.

TABLE 2.

The Range and Mean of Band-Interspace-Band Lengths at Three Middorsal Positions on Specimens from the Seven Populations

	A	B	C	D	E	F	G
N	23	15	13	20	48	25	18
band	12.0-23.0	9.0-16.0	8.0-11.0	7.0-12.0	11.0-22.0	13.0-20.0	14.0-21.0
	$\bar{x}$ 15.9	11.2	9.6	10.1	15.1	16.6	17.5
N	23	15	13	20	50	25	18
interspace	2.0-5.0	2.0-4.5	3.0-4.0	2.5-6.0	2.0-5.0	2.5-6.0	2.0-5.5
	$\bar{x}$ 2.9	3.1	3.3	3.8	3.3	4.5	3.5
N	22	15	12	20	51	25	19
band	8.0-13.0	7.0-12.0	5.0-8.5	5.5-11.0	10.0-19.0	10.0-19.0	11.0-28.0
	$\bar{x}$ 11.0	8.8	7.1	7.5	12.9	14.2	16.1
N	23	15	13	20	51	24	19
band	6.0-16.5	5.0-9.0	4.5-6.0	4.0-6.0	7.5-16.0	8.0-16.0	9.5-16.0
	$\bar{x}$ 9.1	6.6	5.1	5.3	10.3	11.2	12.8
N	23	15	13	20	51	24	17
interspace	2.0-3.0	1.5-4.0	2.0-4.0	2.0-5.0	1.5-6.0	2.0-6.0	1.5-5.0
	$\bar{x}$ 2.7	2.8	3.2	3.2	3.1	3.9	3.6
N	23	15	13	20	51	24	19
band	7.5-13.5	4.0-9.0	4.5-6.0	4.0-7.0	7.0-13.0	8.0-14.5	7.0-16.0
	$\bar{x}$ 9.5	6.1	5.1	5.2	11.5	10.6	12.5
N	24	15	12	20	49	25	19
band	5.0-12.0	4.0-11.0	3.0-5.0	3.0-6.0	6.5-12.5	6.0-10.0	8.0-13.0
	$\bar{x}$ 7.2	6.2	4.0	4.6	8.6	8.3	10.7
N	24	15	10	20	50	25	18
interspace	1.5-4.0	1.5-3.0	1.5-3.0	2.0-4.0	1.0-6.5	2.0-9.0	2.0-6.0
	$\bar{x}$ 2.2	2.2	2.1	3.1	3.1	4.3	3.5
N	24	15	11	20	50	25	19
band	5.5-11.0	4.0-8.0	3.5-6.0	3.0-6.0	5.5-14.0	6.0-12.5	8.0-14.0
	$\bar{x}$ 7.7	5.8	4.5	4.6	8.6	8.8	11.1

There is an average decrease in interspace length from anterior to posterior in all samples except F and G. In the former the midbody interspaces average shorter than the posterior interspaces while in the latter the midbody interspaces average slightly longer than either the anterior or posterior interspaces which are the same (Table 2). Specimens from populations A and B have the smallest mean interspace lengths. Specimens from population F have the longest interspace lengths.

There is no consistent number or location of bands which show signs of splitting or fusion (indicated by light centers) in any population. However, there is some consistency within certain populations in the extent of the light central area. For example, in Oaxaca the light areas within the darker bands are relatively large and diffuse. In Sinaloa the central light areas often form discrete spots.

Collar length.—The length of the light nuchal collar varies among individuals from the same population. In some specimens the first body blotch contacts the posterior margin of the head cap or the parietal scales on the midline or is separated from them by only half a dorsal scale. Others may have

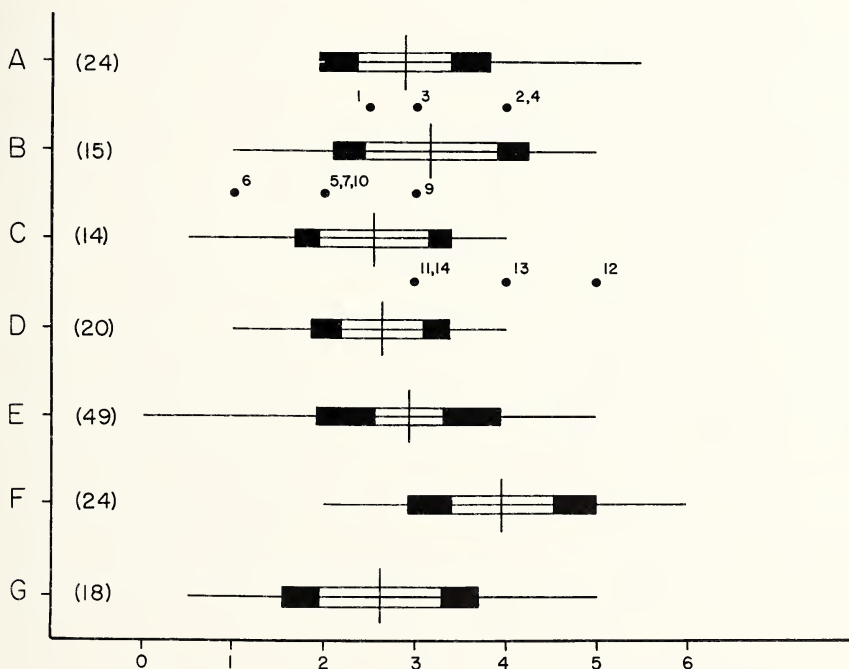


Figure 4. Statistical analysis of the collar lengths in populations A through G of *Trimorphodon tau*. See legend to Figure 2 for explanation of diagrams and symbols.

as many as six dorsal scales separating the first body blotch from the head cap or the parietal scales. However, the collars among the seven samples have nearly the same average lengths as indicated by the number of light scales on the midline (Fig. 4). Only population F has a noticeably higher number of dorsal scales in the nuchal collar. In addition, snakes from population F have the greatest interspace length (Table 2). Most of the specimens from intermediate localities have intermediate collar lengths which fall within the range of variation of the two samples concerned. Notable exceptions, however, are the collar lengths for the type specimens of *T. collaris* and *T. forbesi* which are plotted between populations C and D (Fig. 4, Nos. 12, 13). Both of these have collar lengths most similar to those characteristic of sample F. The type of *Trimorphodon forbesi* has four scales, very near the mean for F, while the type of *T. collaris* has five and is near the upper end of the range of sample F.

Dorsal head cap.—The pattern of dark and light colors on the head generally is consistent within a geographic area. Because of this geographic consistency, a detailed analysis of the head patterns is extremely useful in determining the relationships among the seven samples. Although individual head patterns may be very complex (Figs. 5, 6), they can be analyzed in terms of the following components: snout—light or dark rostral and internasal scales; presence or absence of a prefrontal bar—light bar extending across the prefrontal scales with dark anterior and posterior borders; presence or absence of an interocular (interorbital) bar—a light bar extending between the eyes, usually including the supraocular scales and the frontal scale; presence or absence of a parietal mark—a light mark of various design that may or may not connect to the interorbital bar or the light collar; presence or absence of an occipital spot—a medial, dark rounded spot located on the posterior portion of each parietal scale and the adjacent dorsal scales in the collar; posterior border—the shape of the posterior margin of the dark cap where it is bordered by the light nuchal collar.

Most snakes from population A have dark snouts (a few specimens from near Alamos, Sonora have light snouts) and a light prefrontal bar (blending into the snout of the light snouted forms) that is restricted to the anterior third of the prefrontal scales (Fig. 5A). Occasionally (three specimens) the prefrontal bar is connected with the interorbital bar by a straight or irregular medial area. The interocular bar is always present, usually has irregular borders, and generally is continuous between the orbits (interrupted in two specimens). A parietal mark is always present but extremely variable in shape and extent (Fig. 7). Frequently the parietal mark is shaped like an irregular-armed trident, a bell, a teardrop, or consists of two oblong parts arranged at right angles to form an inverted T. The parietal mark (connected medially to the interorbital bar in one specimen) begins at the posterior edge of the frontal scale and continue posteriorly to connect with the collar (56 percent). In the remaining specimens the parietal mark is separated from the light collar. An

occipital spot is present in 12 of the 14 specimens with the parietal mark-collar connection. The posterior border of the head cap may have a single median indentation (16 specimens), a lateral indentation on either side of a median posterior extension (five specimens), or it may be nearly straight (three specimens).

The two specimens from Ventanas, Durango have complete interorbital

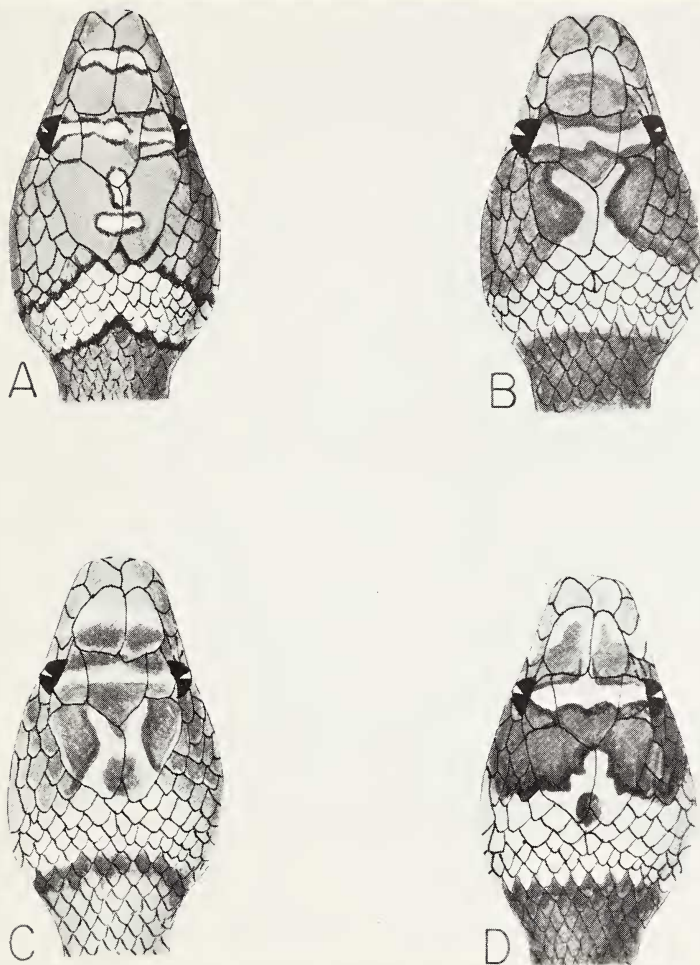


Figure 5. Representative dorsal head cap patterns for specimens of *Trimorphodon tau* from A) Terreros, Sinaloa in population A; B) between Hostotipaquillo and Magdalena, Jalisco in population B; C) S Ciudad Victoria, Tamaulipas in population C; D) intermediate locality at Jalapa, Veracruz.

bars and light snouts that include the area of the prefrontal bar (Fig. 7). The simple parietal marks are restricted to the suture lines between the parietal scales. The parietal mark is connected to the light collar in one specimen and separated in the other. An occipital spot is present in the snake with the parietal mark-collar connection.

The specimen from near San Blas, Nayarit has a dark snout, a prefrontal bar, an interorbital bar, a parietal mark connected to the collar, and an occipital spot. It is very similar to several Sinaloan specimens.

Most snakes from population B have dark snouts (light in the Zacatecas specimen and two Michoacán specimens) and distinct light prefrontal bars (66 percent of individuals). The interorbital bar is present (faint in KU 67735) and complete in all specimens except one (UMMZ 118950), where it is interrupted medially. The arms of the parietal mark, which is usually Y-shaped, edge the frontal scale posteriorly (Fig. 5B; Cope, 1900: fig. 315). The upright base extending posteriorly along the parietal suture may connect to the collar (six specimens) or remain separate from it (five specimens). In one specimen (FMNH 105194) the arms of the parietal mark connect with the interorbital bar on the supraocular scales forming a triangle (Taylor, 1939: pl. 35, fig. 2). The parietal mark is oblong in three snakes and heart-shaped in one. The occipital spot is less common than in population A, being found in only two specimens. The posterior border of the head cap is rounded in two specimens, forms a straight edge in one, is indented medially in five, and has a medial posterior projection in the remaining seven snakes.

A snake from La Cumbre, a locality southwest of population B, has a head pattern very similar to many specimens from B in that it has an interocular bar and a medial posterior projection of the head cap. The snout is somewhat lighter than the rest of the head cap and includes the prefrontal bar. The parietal mark is V-shaped and outlines the frontal scale posteriorly.

Two specimens from Tacúcuaro, Michoacán (southeast of population B) have dark snouts, interorbital bars, and irregular Y-shaped parietal marks that connect to the light collar. An occipital spot is present in one specimen but absent from the other (Fig. 7). Although these two snakes lack prefrontal bars, they are similar in head pattern to other snakes from population B.

Three specimens from Guanajuato (east of population B) have interocular bars and Y-shaped parietal marks characteristic of most specimens from B but resemble the Tacúcuaro specimens in lacking the prefrontal bars. The parietal mark connects to the collar in two specimens and is separate from it in the third. The snout, including the prefrontal bar, is light in one specimen and dark in two.

An Aguascalientes specimen from a locality north of population B has a light snout that includes the prefrontal. In this respect the Aguascalientes snake is similar to one of the Guanajuato specimens and to the Zacatecas specimen in population B. The interorbital bar is complete and the parietal mark, which

is roughly Y-shaped, does not connect to the light collar. The posterior border of the head cap is rounded.

Specimens from sample C have a very complex head pattern. Half of the individuals examined have a light snout that encompasses the prefrontal area. The other specimens have a dark snout with either a well-developed or very faint prefrontal bar. Many specimens, especially those with the lighter snout have a patch of dark color in the center of each prefrontal scale. These patches may be joined medially or separated by a lighter suture line between the prefrontal scales. About half of the specimens have a second light bar on the posterior edges of the prefrontals. The interocular bar is always present and usually expanded on the frontal scale. In one-third of the specimens the interorbital bar is connected anteriorly to the prefrontal bars and posteriorly to the parietal mark. In these specimens the dark head color actually is restricted to six spots, one in the center of each prefrontal scale, one at the anterior edge of each supraocular and adjacent frontal scale, and one on the posterior part of each supraocular and adjoining frontal and parietal scales.

In most of the specimens from Tamaulipas and San Luis Potosí, the arms of the parietal mark form a V and outline the posterior edges of the frontal scale. The posterior part of the parietal mark bifurcates and encloses a large occipital spot before joining the collar (Fig. 5C). In these specimens the posterior border of the head cap is indented medially.

The parietal marks of the four specimens from Hidalgo differ from the more northern representatives of sample C. One specimen (LACM 53023) has a Y-shaped mark outlining the frontal edges and connecting to the collar. It lacks an occipital spot and has a postero-medially indented head cap. In two other specimens (AMNH 93432 and ANSP 14770) the parietal mark is lyre-shaped and not connected to the light collar. The arms of the lyre extend to the frontal borders, connecting with the interorbital bar on one side in one specimen. They do not outline the postero-medial edges of the frontal scale. In both specimens the occipital spot is incorporated into the head cap, thereby extending the posterior border of the cap medially. In the fourth specimen (USNM 110401) the interocular bar extends posteriorly to the tip of the frontal scale. The parietal mark is fragmented into three parts. On the left side the mark borders the frontal anteriorly and extends posteriorly nearly to the light collar forming a shallow, laterally concave arc. On the right side only the anterior half of the arc is present. The posterior half consists of a light rounded spot on the posterior part of the right parietal scale, just above the light collar. The posterior border of the head collar is nearly straight medially but rounded laterally.

A specimen from Jalapa, Veracruz has a light snout extending over the anterior half of the prefrontals. Each nasal scale is very faintly pigmented. The interorbital bar is complete and connects medially to the light snout along the prefrontal suture. The parietal mark is irregular in shape, restricted to the

parietal suture (Fig. 5D) and connected to the light collar. The occipital spot is well defined.

The type specimen of *Trimorphodon collaris* lacks pigment on the internasal scales. Its interocular bar is broken about the middle of each supraocular, and it has a more rectangular-shaped parietal mark connected to the collar. In other respects it is very similar to the Jalapa specimen.

The type specimens of *Trimorphodon tau* and *T. forbesi* also are from localities in the Atlantic versant and generally are similar to the two specimens mentioned above. The type of *T. tau* has dark circular marks in the center of each internasal scale. The light snout is connected medially and laterally with the prefrontal bar which is also connected with the complete interocular bar along the suture between the prefrontals. The lighter color of the collar continues onto the temporal parts of the head connecting with the postero-lateral portions of the interocular bar. As a result, the dark parietal portion of the head cap is greatly restricted and completely surrounded by the lighter coloration. The parietal mark is connected to the collar. Posteriorly the head cap is nearly straight. The occipital spot is present but small. The type of *T. forbesi* also has a lighter snout that includes the prefrontal area. The interocular bar is complete and connects along the prefrontal suture to the lighter snout. The parietal mark is rounded and broadly joined to the light collar. The occipital spot is small. The posterior border of the head cap is rounded laterally and indented medially. In general these four specimens from eastern México (Veracruz, Puebla, Oaxaca) are very similar in overall head pattern.

The head patterns of specimens from population D generally are more uniform than are those from population C. Most of the specimens (75 percent) have a dark snout and lack a prefrontal bar. Two of the five individuals with a light snout have dark pigment in the central parts of the internasal scales and a suggestion of a prefrontal bar. In this respect they are similar to the type of *Trimorphodon tau*. In several specimens, including light-snouted and dark-snouted individuals, the edges of the internasal and prefrontal scales are lighter than the central portions (Fig. 6A). Ten specimens have a light bar along the suture between the prefrontals. Often this bar is connected to the interocular bar (50 percent) forming the inverted T-pattern characteristic of *Trimorphodon tau* (Cope, 1869: 152). The interocular bar is always present and frequently (50 percent) extends laterally to the orbits. In some specimens (eight of 20) the interocular bar forms a shallow arc, concave posteriorly. The parietal mark has a simple configuration, rarely touching the frontal scale, and is connected with the light collar in all but two specimens (Taylor, 1940: fig. 8). In one specimen (AMNH 10093) the mark is irregular in shape (two lateral arms on each side) and contacts the posterior part of the frontal scale. An occipital spot is present in only five specimens.

The head cap is indented medially in all but two specimens from sample D. In these two specimens the parietal mark and the collar do not connect, and

thus the head cap extends postero-medially. The white collar extends anteriorly along the sides of the head in these specimens, together with 16 of the 18 indented head cap forms, giving the head cap a rounded appearance. In two (Fig. 7) the postero-lateral edges of the cap are nearly straight.

We examined the head patterns of 48 snakes from population E. In only eight of these does the light snout include the prefrontal bar area. Although the

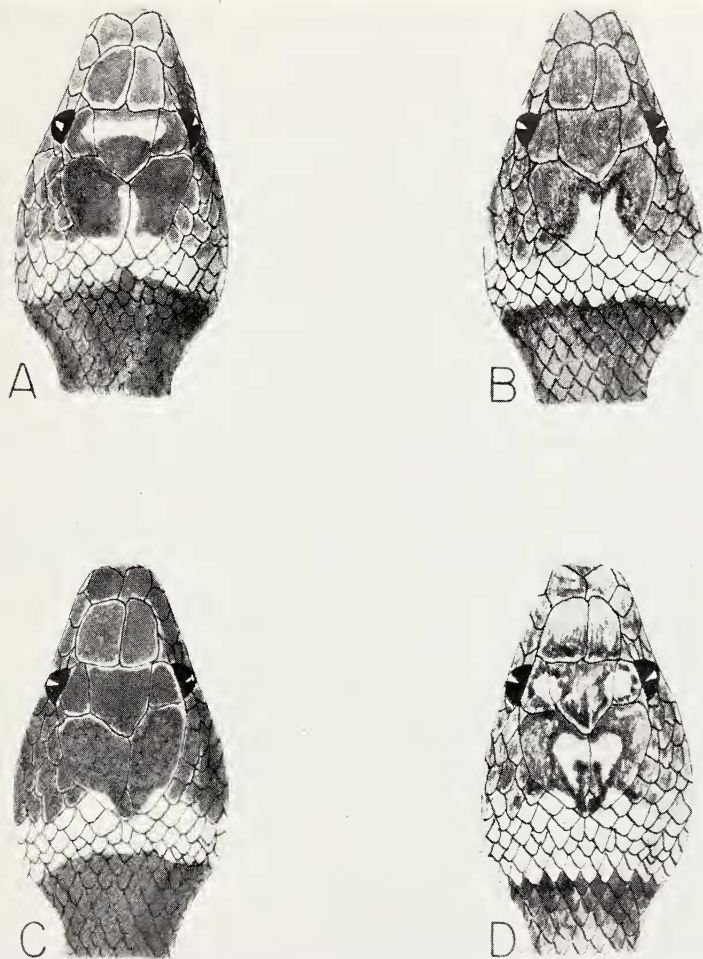


Figure 6. Representative dorsal head cap patterns for specimens of *Trimorphodon tau* from A) 3 mi NE Mitla, Oaxaca in population D; B) Chilpancingo, Guerrero in population E; C) Coalcomán, Michoacán in population G; D) 4 mi S Autlán, Jalisco in population G.

snout in these few specimens is somewhat lighter than the rest of the cap, it is still well pigmented and not the white or very light tan characteristic of certain light-snouted specimens from populations A and C. None have a defined prefrontal bar, although three individuals have a pair of light spots on the anterior prefrontal scales. Three other specimens have a medial light spot on the prefrontal suture. An interorbital bar is lacking in 23 specimens, reduced to a median frontal spot or to two lateral supraocular spots in 21 specimens, and complete in four specimens. None has a connection between the interorbital bar and parietal mark. In all specimens, except four, the parietal mark is connected to the light collar (Fig. 6B) or is absent. Of these four, two have a small circular spot on the parietal suture, one has a small central and two small lateral spots, and the fourth has two lateral spots that appear to be remnants of a V-shaped mark. Of the remaining 44 specimens, eight have no indication of a parietal mark; the posterior margins of their head caps are rounded laterally (Fig. 7). Most of the others have a median extension of the collar connecting to the parietal mark. Usually the parietal mark or anterior end of the collar extension is rounded, but occasionally it may be Y- or V-shaped or may narrow rapidly at its anterior apex near the frontal scale. Occasionally (six specimens) the collar has a double extension onto the parietal region, and the head cap extends posteriorly on the midline. The head cap is rounded laterally in nearly all of these specimens. An occipital spot is present in only nine.

In twelve of 24 specimens from sample F, the snout is lighter than the rest of the head cap and includes the prefrontal bar area. In this respect they are similar to the light-snouted individuals of population E. Only two of the dark snouted specimens have a prefrontal bar. When a complete interorbital bar is present (three specimens), it is faint. In twelve other snakes, the bar is fragmented or reduced to one, two, or three circular spots or short bars. There is not interorbital bar in nine specimens (Taylor, 1940: pl. 52). Four specimens lack parietal marks and have a head cap with a rounded posterior margin. Three specimens have shallow V-shaped parietal marks that outline the frontal scale and are not connected with the light collar. In these specimens the posterior edge of the head cap has a single medial indentation, two lateral indentations, or a postero-medial extension. In the remaining snakes (17) the parietal mark is connected to the collar, and thereby, the posterior edge of the head cap is indented medially. The extended collar-parietal mark may be broadly Y-shaped (Fig. 7), triangular, narrow and restricted to the parietal suture, or wishbone-shaped. There is a large distinct occipital spot in the collar extension in most (12 of 17) of these specimens.

The head patterns are remarkably consistent in population G. None, except the type of *T. fasciolata*, have a light snout or show any trace of a prefrontal bar. In the type specimen of *T. fasciolata* the snout and the edges of the prefrontal scales are somewhat lighter than the rest of the head cap. An interorbital bar is lacking in all specimens (Fig. 6C) except three. In two of these

(UMMZ 112516 and the type of *T. fasciolata*) the supraocular scales have light centers. The third specimen from Autlán, Jalisco (KU 27191) has two light circular spots in the interorbital area. Distinct parietal marks are lacking from all except the Autlán specimen (Fig. 6D) and a specimen from near Apatzingán (UMMZ 112515). In the latter there are two small spots on the posterior third of each parietal scale. The posterior margin of the head cap is indented in one specimen from Apatzingán (FMNH 37079) and the type of *T. fasciolata* and shallowly indented in a third (UMMZ 104696). Occipital spots, lacking in other specimens, are present in these three snakes. The posterior margin of the head cap is doubly indented in nine specimens (Fig. 6C), rounded in four, nearly straight in two, and slightly convex in one.

The geographic distribution of the different head patterns is illustrated in Figure 7.

Coloration.—These snakes have considerable variation in coloration from sample to sample and within some samples. Because adequate color descriptions and pictures of specimens from many areas are available in the literature (Taylor, 1939: 364-367; 1940: 474-479; Smith, 1941: 161-167; Peters, 1954: 33; Davis and Dixon, 1957: 24; Duellman, 1961: 111; Brown and Brown,



Figure 7. Geographic distribution of representative head cap patterns for specimens of *Trimorphodon tau* from localities within the seven samples and selected intermediate localities.

1967: 325), no detailed color description will be included here. Instead we will summarize this information and present it together with color notes on living specimens from Sinaloa and Puebla.

The ground color of adults ranges from various shades of brown to fawn, pale tan or gray, usually becoming darker posteriorly. Juveniles often have a more reddish or grayish ground color than do the adults. The cross bands of both age groups are darker than the ground color and often yellow-brown or gray-brown to black. In many specimens the center of each band is lighter. The edges of each band are usually bordered with dark brown or black. Juveniles apparently have darker bands than adults from the same area. Laterally, smaller dark blotches are present in the interspaces of some specimens. The head cap is brown, gray-brown or black and nearly the same color as the cross bands. The lips, chin and throat usually are tan or white. The venter may be tan or creamy white, and often with a reddish or salmon tinge posteriorly. In some snakes the venter is mottled by ventral extensions of the cross bands and interspace blotches; in others the venter may be spotted. Some have a nearly immaculate belly. In some juveniles the ventral surface of the tail may be nearly black.

The iris may be yellow-brown, gray-brown or grayish-tan.

DISCUSSION

CHARACTER ANALYSIS

Much similarity exists among the seven samples. Some characters indicate independent, discordant patterns of variation. Even though most characters are not diagnostic, three are particularly useful in deducing the relationships among the seven samples: number of ventral plus subcaudal scales, number of dorsal body bands, and dorsal head cap pattern.

The number of ventral-subcaudal scales decreases from north to south in samples A through C. The trend continues southward into population D, where the lowest counts are recorded. Two specimens (Fig. 2, Nos. 11, 14) from intermediate areas between C and D are more similar to D than to C in this character, while two other specimens from intermediate areas (Fig. 2, Nos. 12, 13) are more similar to C and F than they are to D. This suggests a connection among the samples through the high river valleys of southeastern Puebla and Oaxaca. Population G has the highest counts and is the most northern of the three Balsas-Tepalcatepec Basin samples. In this character sample G approached sample B, its closest geographic neighbor. The ventral-subcaudal scale counts will not allow for absolute distinction between specimens from geographically adjacent samples.

An analysis of the number of dorsal cross bands (Fig. 3) gives a slightly different picture of the relationships among the seven samples. Among populations A, B, and C there is an increase in number of dorsal blotches from northwest to southeast. The geographically intermediate specimens generally con-

firm this trend. Sample D has fewer bands than does C and thus has a slightly different relationship to A, B, and C in this character than it did in terms of ventral-subcaudal scales. In this respect, however, the number of dorsal blotches of sample D approaches those characteristic of samples E and F. Of the four specimens from eastern México that are geographically intermediate among samples C, D and F, three (Fig. 3, Nos. 11, 13, 14) have counts most similar to the counts of D while the fourth (Fig. 3, No. 12) has a count most like those of sample F.

In dorsal cross bands E, F and G are closely related to each other and well differentiated from sample D. The most striking thing about the dorsal band counts is the difference between samples G and B which do not approach each other even though the two populations are closely adjacent (Fig. 3). This is a notable exception to their similarity in the number of ventral-subcaudal scales.

The same general relationship is present in the seven samples for both dorsal head patterns and dorsal cross bands. An interocular bar, usually complete, and a discrete parietal mark are always present in specimens from samples A, B, C, and D. The remnants of an interocular bar are present in 43 of 91 specimens from samples E, F and G. Only seven specimens from the Balsas-Tepalcatepec samples have a complete interocular bar. A discrete parietal mark, that is one not connected to the collar, is found only in nine of the 91 specimens in samples E, F and G. A prefrontal bar or light snout including the area of the prefrontal bar is found in most snakes from samples A, B and C. In sample D a prefrontal bar is usually lacking, as it is in most specimens from samples E and G. Approximately 50 percent of the specimens from sample F have light snouts that include the area of the prefrontal bar and thus are somewhat intermediate between samples A, B, C and D, E, G.

In summary, the Balsas-Tepalcatepec Basin samples (E, F and G) have a darker, more uniform head cap than is found in specimens from samples A, B, C and D. The Balsas-Tepalcatepec samples generally lack the prefrontal and interocular bars and the discrete parietal marks characteristic of the other samples. In general they lack the ornate head marking characteristic of the other four populations. Except for two snakes (KU 27191 and USNM 110400), there is no indication of any similarity between samples B and G in characters of head pattern. Some specimens from samples E and F show an apparent relationship to samples C and D by possessing remnants of an interocular bar and parietal mark. The head patterns of specimens from areas geographically intermediate between samples A, B, C and D have intermediate head patterns.

TYPE SPECIMENS

It seems appropriate to discuss briefly the six type specimens with reference to our seven populations to clarify our systematic treatment of the various samples.

The type specimen of *Trimorphodon tau* is a small snake in relatively poor condition. It was adequately described by Cope (1869) and redescribed by Taylor (1939). Although from a locality northwest of sample D, in all characteristics, it is typical of specimens from that sample.

The holotype of *Trimorphodon upsilon* is typical in all respects of specimens from sample B and was included in that unit. Zweifel (1959) noted that many of the specimens collected by Major probably did not come from Guadalajara, Jalisco as the locality information indicated but possibly were from Colima. However, Zweifel did point out that the type of *Trimorphodon upsilon* may actually have been from Guadalajara as additional specimens of this species are known from the same general area. Our analysis supports Zweifel's contention that Guadalajara probably is the type locality as originally stated.

The cotypes of *Trimorphodon latifascia* from Puebla have the characteristics typical of Puebla specimens from sample F. However, they were not included in sample F because the specific type locality is unknown (Peters, 1869).

For purposes of nomenclatural stability and in accord with Article 74, International Commission on Zoological Nomenclature (1964), we designate ZMB 6652a, the larger of the two syntypes (588 mm total length), as the lectotype. The smaller specimen (417 mm total length), ZMB 6652b, is designated the paralectotype in accord with recommendation 74E. Both specimens are males and have 211, 209 ventrals, 79, 74 subcaudals, and 21, 22 dorsal body bands. The snout is slightly lighter than the head cap in both specimens. In one the interocular bar consists of two short lateral spots and in the other of a median spot. The posterior border of the head cap is indented medially and rounded laterally in both. A faint occipital spot is present in the smaller paralectotype.

The holotype of *Trimorphodon collaris*, like the type of *T. tau*, is a juvenile. Cope's description (1875) is accurate for the characters listed. Some confusion exists concerning the type locality and number of specimens (see Historical Review and Smith, 1941: 166). This specimen, although from a locality somewhat intermediate among samples C, D and F, is typical of specimens from sample F in the important characteristics of ventral plus subcaudal scales, collar length, and number of dorsal blotches. The band-interspace-band lengths also are closest to those characteristic of sample F. The head pattern is similar to the patterns found on specimens from both D and F, although it is more similar to those from D. We consider the specimen to be most similar to snakes from sample F.

The type specimen of *Trimorphodon fasciolata* is a large male collected from a locality on the northeastern periphery of sample G. The specimen was adequately described by Smith (1941: 160-162). In all characteristics except certain details of head pattern (see previous description), it is typical of rep-

representatives of sample G, in which it was included. These differences in head pattern emphasize the marginal nature of the locality and may reflect its proximity to specimens from sample B and the intermediate specimens from Tacicuaró, Michoacán.

Finally, the type of *Trimorphodon forbesi* is an exceptionally large male that is relatively well preserved but badly faded. In general our findings, on examination of the type, agree well with Smith's description (1941: 163-165) with two exceptions. We recorded five more ventrals and two more subcaudals than listed in the type description. Unfortunately the ventral scales are damaged in some areas and accurate counts are difficult to make. This may account for the discrepancies. However, we believe our count of 297 scales to be accurate.

The other point with which we disagree is Smith's (1941: 164-165) discussion of and reference to the "pattern reversal" characteristic of *Trimorphodon forbesi*. It is quite obvious that this specimen is faded; apparently the brown color of the head pattern faded more rapidly than did the dark borders along the interocular bar and nuchal collar, thus giving the appearance of a light head pattern with a darker interocular bar and nuchal collar. We cannot accept the contention that this is anything other than a badly faded but originally normally colored head pattern. The pattern itself is similar to the pattern of the type of *Trimorphodon tau* and other specimens in sample D.

The remaining characters of *forbesi* that Smith (1941: 165) used to distinguish it from other species include a divided anterior loreal, the fifth and sixth labials entering the eye, a faintly marked belly and white subcaudal surface, the number of cross bands, the narrow black borders of the cross bands, and the length of the cross bands on the mid-dorsal line. All of these characteristics are known from other samples (see previous description of geographic variation) and therefore are of little value in distinguishing this specimen. In ventral-subcaudal scales and collar length this specimen is more similar to sample F. In number of dorsal blotches and in head pattern, it is more similar to sample D. Certain characteristics of head scales and blotch length are intermediate between those for samples D and F.

Thus, the type of *Trimorphodon forbesi* has some characters typical of specimens from sample D, some typical of specimens from sample F, and some that are intermediate. Because of its intermediate locality and characteristics, we consider the specimen to represent a population of *Trimorphodon* that apparently bridges the gap between samples D and F.

In order to evaluate the usefulness of the three characters, ventral-subcaudal scales, body bands and head cap pattern, as indications of phylogenetic relationship, we attempted to correlate their geographic variation with various environmental parameters. Klauber (1941) showed that desert specimens consistently tend to have more ventral scales than coastal specimens of the same species. He also found that specimens of *Trimorphodon vandenburghi* from

the desert had more dorsal blotches than those along the coast. Klauber attributed these disparities to differences in humidity, and possibly temperature. Fox (1948) showed how different temperature regimes can influence scutellation in developing embryos of *Thamnophis*. Gravid females from the same natural population kept at cooler temperatures give birth to young with significantly fewer ventral and subcaudal scales than young from females maintained at warmer temperatures. Stebbins (1949) suggested that physical factors of humidity, temperature and light are important considerations determining the coloration and pattern of the salamander *Ensatina*.

In our analysis we could find no consistent correlation between environmental factors of temperature, rainfall or elevation and the geographic variation in ventral-subcaudal scales, dorsal cross bands or head pattern. In some samples there appeared to be a positive correlation between ventral-subcaudal scales and temperature; in other samples the same character indicated an inverse relationship to mean temperature. These same results generally were found in other comparisons. Unfortunately, the lack of precise microenvironmental information for many areas prevents detailed analysis of the possible correlation between other environmental factors and morphology.

Band lengths (Table 2) and band numbers (Fig. 3) have an inverse relationship. As the average band length increases, the number of bands decreases, and the snakes have a greater dark to light ratio. This is found in samples E, F, and G and is exemplified also by their darker head pattern. The Balsas-Tepalcatepec Basin is characterized by both high mean annual temperatures and high mean annual rainfall (Vivó Escoto, 1964). This suggests that a detailed analysis might show a correlation between mean annual temperature, rainfall, and/or light intensity and the number of dorsal bands and head pattern. Details of vegetation type and density would also have to be considered.

Variation in band numbers among the samples may be the result of splitting or fusion of some of the cross bands. For example, there is an average increase of five body bands from population A to B, but a decrease of about 15 scale lengths (difference between totals of six band lengths in Table 2). Although the light centers of many bands suggest splitting or fusion, there is no consistent location or number of bands which have light centers within any population. In addition, we were unable to derive the various band patterns from one another. It seems unlikely, therefore, that the light centers characteristic of many cross bands are indicative of fusion or division, a possible means of decreasing or increasing the band number. Differences in cross band numbers and lengths may represent adaptive responses to different selective pressures that increase or decrease the overall ratios between dark and light areas on the snakes.

SYSTEMATIC TREATMENT

Our data indicate overall similarities among the seven samples and the type specimens in nearly all characteristics examined. The analyses reveal

a geographic trend towards a southern reduction in ventral-subcaudal scales among samples A, B, C and D and among samples E, F and G, and also point to the similarities among samples A, B, C and D and samples E, F and G in number of body bands and head pattern. Specimens with characteristics that are intermediate between these two groups indicate that only a single species is involved. Therefore, we refer our seven samples, their intermediates, and the types of *Trimorphodon tau*, *upsilon*, *collaris*, *latifascia*, *fasciolata* and *forbesi* to one species. After careful consideration and consultation, we conclude that Günther's (1895) use of *Trimorphodon upsilon* did not constitute the action of the first revisor as defined in Article 24, International Code of Zoological Nomenclature. Therefore, the name *Trimorphodon tau* is applicable because of the action of Smith and Darling (1952) who gave priority to *tau* rather than *upsilon*, by their action as first revisor.

TRIMORPHODON TAU COPE

Trimorphodon tau Cope, 1869, Proc. Amer. Phil. Soc., 11, p. 152 (type description; type locality "western part of the Isthmus of Tehuantepec, Mexico," in error); 1875, J. Acad. Natur. Sci. Philadelphia, ser. 2, 8, p. 131. Sumichrast, 1892, La Naturaleza, 6(2), p. 44 (type from Quiotepec, between Tehuacán and Oaxaca). Cope, 1886, Proc. Amer. Phil. Soc., 23, p. 286; 1887, Bull. U.S. Natl. Mus., 32 p. 68; 1892, Proc. U.S. Natl. Mus., 14, p. 678. Günther, 1895, Biologia Centrali-Americana, Reptilia, p. 174. Boulenger, 1896, Catalogue of the snakes in the British Museum, vol. 3, p. 56. Mocquard, 1899, Bull. Soc. Phil., ser. 9, 1, p. 157. Cope, 1900, Rep. U.S. Natl. Mus. for 1898, p. 1101. Gadow, 1905, Proc. Zool. Soc. London, 1905, p. 224. Mocquard, 1908, in Duméril and Bocourt, Mission Scientifique au Mexique et dans l'Amerique Centrale, 3, pp. 908, 912. do Amaral, 1929, Mem. Inst. Butantan, 4, p. 202. Taylor, 1939, Univ. Kansas Sci. Bull., 25, pp. 366-67; 1940, Univ. Kansas Sci. Bull., 26, pp. 474-77, fig. 8, plate 51. Smith, 1941, Proc. U.S. Natl. Mus., 91, pp. 166-67; 1943, Proc. U.S. Natl. Mus., 93, p. 494. Smith and Taylor, 1945, Bull. U.S. Natl. Mus., 187, p. 148. Taylor, 1949, Univ. Kansas Sci. Bull., 33, pp. 210-11. Davis and Dixon, 1957, Southwestern Natur., 2, p. 24. Martin, 1958, Misc. Publ. Mus. Zool. Univ. Michigan, 101, p. 74. Duellman, 1961, Univ. Kansas Publ. Mus. Nat. Hist., 15, p. 112; 1965, Univ. Kansas Publ. Mus. Nat. Hist., 15, pp. 655, 657, 660-61, 666, 685. Lynch and Smith, 1965, Herpetologica, 21, p. 168. Brown and Brown, 1967, Texas J. Sci., 29, p. 325.

Eteirodipsas biscutata (in part), Jan, 1863, Elenco sistematico degli ofidi . . . , p. 105. Jan and Sordelli, 1872, Iconographic generale des ophiidiens, vol. 3, livr. 39, plate 1, fig. 3. Cope, 1892, Proc. U.S. Natl. Mus., 14, p. 679 (footnote). Günther, 1895, Biologia Centrali-Americana, Reptilia, p. 175.

Trimorphodon upsilon Cope, 1869, Proc. Amer. Phil. Soc., 11, p. 152 (type description; type locality "Guadalajara, West Mexico"); 1875, J. Acad.

Natur. Sci. Philadelphia, ser. 2, 8, p. 131; 1886, Proc. Amer. Phil. Soc., 23, p. 286; 1887, Bull. U.S. Natl. Mus., 32, p. 68; 1892, Proc. U.S. Natl. Mus., 14, p. 678. Günther, 1895, Biologia Centrali-Americana, Reptilia, pp. 174-75. Boulenger, 1896, Catalogue of the snakes in the British Museum, vol. 3, p. 55. Mocquard, 1899, Bull. Soc. Phil., ser. 9, 1, p. 157. Cope, 1900, Rep. U.S. Natl. Mus. for 1898, pp. 1104-1105, fig. 315. Gadow, 1905, Proc. Zool. Soc. London, 1905, pp. 196, 231, 233; 1910, Zool. Jahrbuch, 29, pp. 697, 701. Mocquard, 1908, in Duméril and Bocourt, Mission Scientifique au Mexique et dans l'Amerique Centrale, 3, pp. 908, 910-11. do Amaral, 1929, Mem. Inst. Butantan, 4, p. 202. Taylor, 1939, Univ. Kansas Sci. Bull., 25, pp. 365-66, plate 35, fig. 2. Smith, 1941, Proc. U.S. Natl. Mus., 91, pp. 162-163; 1943, Proc. U.S. Natl. Mus., 93, p. 494. Smith and Taylor, 1945, Bull. U.S. Natl. Mus., 187, p. 148. Zweifel and Norris, 1955, Amer. Midland Natur., 54, p. 245. Duellman, 1961, Univ. Kansas Publ. Mus. Nat. Hist., 15, p. 112.

Dipsas biscutatus var. *latifascia* Peters, 1869, Monatsber. Akad. Wiss. Berlin, p. 877 (type description; type locality, Puebla, México).

Trimorphodon collaris Cope, 1875, J. Acad. Natur. Sci. Philadelphia, ser. 2, 8, p. 131 (type description; type locality "Orizaba, Vera Cruz"). Sumichrast, 1882, La Naturaleza 6(2), p. 44 (type(s) came from Tuxpango, near Orizaba); Cope, 1886, Proc. Amer. Phil. Soc., 23, p. 286; 1887, Bull. U.S. Natl. Mus., 32, p. 68; 1892, Proc. U.S. Natl. Mus., 14, p. 679. Günther, 1895, Biologia Centrali-Americana, Reptilia, p. 174. Cope, 1900, Rep. U.S. Natl. Mus. for 1898, p. 1101. Taylor, 1939, Univ. Kansas Sci. Bull., 25, pp. 364-65. Smith, 1941, Proc. U.S. Natl. Mus., 91, pp. 165-66; 1943, Proc. U.S. Natl. Mus., 93, p. 493. Smith and Taylor, 1945, Bull. U.S. Natl. Mus., 187, p. 147.

Sibon biscutatus, Garman, 1883, Mem. Mus. Comp. Zool. Harvard Univ., 8, pp. 16, 134 (part).

Sibon biscutatum var. *latifasciatum*, Garman, 1883, Mem. Mus. Comp. Zool. Harvard Univ., 8, pp. 16-17, 134.

Sibon upsilon, Garman, 1883, Mem. Mus. Comp. Zool. Harvard Univ., 8, p. 134.

Trimorphodon biscutatus, Günther, 1895, Biologia Centrali-Americana, Reptilia, p. 174 (part).

Trimorphodon upsilon var. *collaris*, Mocquard, 1908, in Duméril and Bocourt, Mission Scientifique au Mexique et dans l'Amerique Centrale, 3, plate 74, fig. 2, a, b.

Trimorphodon latifascia, Taylor, 1939, Univ. Kansas Sci. Bull. 25, pp. 364-65, plate 36, fig. 2; 1940, Univ. Kansas Sci. Bull., 26, p. 479, plate 52. Smith, 1941, Proc. U.S. Natl. Mus., 91, p. 160. Smith and Taylor, 1945, Bull. U.S. Natl. Mus., 187, p. 148. Schmidt and Shannon, 1947, Fieldiana Zool. Chicago Nat. Hist. Mus., 31, p. 83. Hall, 1951, Univ. Kansas Sci. Bull., 34, pp. 207-08. Davis and Smith, 1953, Herpetologica, 8, p. 140. Peters, 1954, Occ. Papers Mus. Zool. Univ. Michigan, 554, p. 32. Davis and Dixon, 1957, South-

western Natur., 2, p. 23. Webb and Fugler, 1957, *Herpetologica*, 13, p. 33. Duellman, 1958, *Occ. Papers Mus. Zool. Univ. Michigan* 589, p. 12. Davis and Dixon, 1959, *Proc. Biol. Soc. Washington*, 72, p. 88. Duellman, 1961, *Univ. Kansas Publ. Mus. Natur. Hist.*, 15, pp. 111-12. Fouquette and Rossman, 1963, *Herpetologica*, 19, p. 199. Duellman, 1965, *Univ. Kansas Publ. Mus. Nat. Hist.*, 15, pp. 655-56, 659, 680, 699.

Trimorphodon fasciolata Smith, 1941, *Proc. U.S. Natl. Mus.*, (type description; type locality "near Zaráracua [sic] Falls, 6 kilometers southeast of Uruapan, Michoacán.") 91, pp. 160-62; 1943, *Proc. U.S. Natl. Mus.*, 93, p. 493. Smith and Taylor, 1945, *Bull. U.S. Natl. Mus.*, 187, p. 147. Schmidt and Shannon, 1947, *Fieldiana Zool. Chicago Nat. Hist. Mus.*, 31, p. 83. Davis and Smith, 1953, *Herpetologica*, 8, p. 140. Peters, 1954, *Occ. Papers Mus. Zool. Univ. Michigan*, 554, pp. 32-34. Davis and Dixon, 1957, *Southwestern Natur.* 2, p. 23.

Trimorphodon forbesi Smith, 1941, *Proc. U.S. Natl. Mus.*, 91, pp. 163-65 (type description; type locality "from San Diego [about 5 miles south of Tehuacán], Puebla"); 1943, *Proc. U.S. Natl. Mus.*, 93, p. 493. Smith and Taylor, 1945, *Bull. U.S. Natl. Mus.*, 187, p. 147.

Trimorphodon tau tau, Smith and Darling, 1952, *Herpetologica*, 8, p. 85.

Trimorphodon tau upsilon, Smith and Darling, 1952, *Herpetologica*, 8, p. 85. Zweifel, 1959, *Amer. Mus. Novitates*, 1949, pp. 3-4, 6-8.

Description.—A species of *Trimorphodon* with 201-231 ventral and 61-85 subcaudal scales in males; 210-243 ventrals and 55-80 subcaudals in females; 265-319 total ventral-subcaudal scales; a divided anal scale; usually 3 (2-5) loreal scales, 3 (1-4) preocular, 3 (2-4) postocular, 3 (1-5) primary temporal, 4 (2-5) secondary temporal, 8 (7-10) supralabial with the fourth and fifth (third-sixth) bordering the eye, and 12 (9-14) infralabial scales usually separated from the chin shields at the sixth (fourth-seventh) infralabial; dorsal scales usually in 22, 23, or 24 (21-27) rows at one head length behind the head, 22 or 23 (17-25) rows at midbody, and 15 or 16 (14-18) rows at one head length in front of the anus.

The snakes are usually gray, tan or light brown in ground color and crossed by 18-46 body bands that usually reach the edges of the ventral and subcaudal scales. The cross bands are various shades of brown or black and often darkest along their margins. Most dark cross bands have lighter central areas that approach the ground color. These central areas may be large and diffuse or concentrated into discrete spots. They suggest the splitting of one band or fusion of two bands. The cross bands decrease in length on the midline from anterior to posterior. Often the first cross band is considerably larger than the second. The cross bands are widest dorsally and taper to a broad or narrow base laterally. Laterally, small, irregular interband spots may be present. Frequently the body bands continue onto the abdominal scales giving

the ventral surface an irregular blotched pattern. However, in some specimens the abdominal scales are irregularly spotted or nearly immaculate.

The head pattern is extremely variable (see discussion). It consists of a dark head cap extending from the snout to the posterior parts of the parietals where it usually is separated from the first cross band by a light nuchal collar. In some specimens the snout is light. There may be a prefrontal bar, an interocular bar, a parietal mark and an occipital spot or any combination of these components. In some specimens most or all of the head cap components may be lacking, and the head is uniformly dark brown.

The nuchal collar sometimes extends medially onto the parietal area to connect with the parietal mark. In this instance the anterior border of the collar is chevron-shaped. Often the nuchal collar is straight or slightly indented anteromedially. The posterior border of the collar is nearly always straight. The first body blotch occasionally contacts the head cap or may be separated from it one-half to six dorsal scales. The collar is usually three scales long on the midline.

Subspecies.—The numbers of cross bands, the cross band lengths, and the head pattern indicate that gene flow between samples B and G is limited. The geographic barrier of the Transverse Volcanic Range separating these two samples may be partly or wholly responsible for this apparent restriction of gene flow. Presumably these two populations have come into secondary contact after experiencing separate histories. In our opinion, these two samples do not represent a continuum that was split into two components by the uplift of the Transverse Volcanic Range. It seems more likely that population G evolved from ancestors that moved into the Tepalcatepec Basin from the south after the Transverse Volcanic Range reached its present height in Jalisco and Michoacán (see discussion below). The similarities between the Balsas-Tepalcatepec samples E, F and G and their differences from A, B, C and D support this view. The latter four samples are similar in several characteristics and probably are representative of a continuum, as indicated by specimens from intermediate localities. There appears to have been some genetic exchange between the two groups through samples F and D in some of the river valleys of southeastern Puebla, northeastern Oaxaca and eastern Veracruz.

The similarities and differences between A, B, C and D and between E, F and G have been thoroughly discussed. Consideration of these points, combined with the apparent geographic barriers between these two groups, at this time leads us to recognize them as subspecies. The specimens representative of samples A, B, C and D and their intermediates are referred to *Trimorphodon tau tau*. The specimens from samples E, F and G in the Balsas-Tepalcatepec Basin are referred to *Trimorphodon tau latifascia* (new combination).

Distribution and ecology.—*Trimorphodon tau* is widely distributed along the coastal slopes and foothills of the Sierra Madre Occidental and Sierra Madre Oriental (Fig. 1). Occasional specimens have been taken on the coastal

plains. The species is found in suitable habitats to the north of the Transverse Volcanic Range and the high southern portions of the Mexican Plateau. *Trimorphodon tau* has also been recorded from scattered localities to the east and south of the Mexican Plateau, from the Valley of Oaxaca south and east of the Sierra Madre del Sur. The species is widely distributed in the foothills of the Balsas and Tepalcatepec Basins. Although the species is reported from localities ranging from 100 to 2600 meters in elevation, most of the range of the species lies between 1000 and 2100 meters.

The lack of adequate material from localities between samples A and B, between samples D and E, and between samples E and G probably reflects the inaccessibility of these areas as well as inadequate sampling of suitable habitat. Only four specimens are known from the eastern versant between samples C and D. We suspect that local climatic factors (high annual precipitation and abundant cloud cover) probably restrict the distribution of *Trimorphodon* to drier, less accessible habitats in this area.

Trimorphodon tau is a nocturnal species that occupies semi-arid to seasonally dry habitats. Specimens have been collected in arid tropical scrub, thorn woodland, tropical deciduous forest, mesquite grassland and dry pine-oak woodland (vegetation classifications follow Leopold, 1950). The species is terrestrial and commonly found in rocky areas of irregular relief. Individuals have been collected from beneath rocks, in holes and under bark on fence posts and dead trees during the day and in a flooded rice field at night. Most specimens were found on roads at night. The species feeds primarily on lizards, although frogs and small mammals probably are eaten also. Unidentifiable species of *Sceloporus* and *Cnemidophorus* were found in specimens from Guerrero, Michoacán and Oaxaca.

Eggs and young.—Because very little is known concerning the eggs and young of oviparous snakes, the following data for *Trimorphodon tau* are appropriate.

On July 18, 1966 a large female *Trimorphodon tau* (MVZ 81354) was collected 26 miles NW of Huajapan de León on México Highway 190 in Puebla (Sample F) by J. L. LaPointe. Sometime between the date of capture and July 25, this snake deposited seven eggs. The eggs were incubated following the technique outlined by Zweifel (1961: 112-113). On September 25, one of the eggs was opened and found to be developing. On October 10, the eggs averaged 26.1 mm in length, 16.8 mm in width and 4.0 gm in weight. Five of the remaining six eggs hatched between October 29 and November 1, at least 96 days after laying. The hatchlings made from 2-7 ($x = 5.4$) longitudinal slits in the egg shell to escape. The sixth egg did not hatch and was found, on November 4, to contain a well developed, but dead, female (MVZ 81361). Pertinent information for the mother and five hatchlings are presented in Table 3.

The hatchling snakes are typical of sample F in the characteristics studied.

TABLE 3.
Data for Adult Female and Five Offspring of
Trimorphodon tau from Puebla, México

Specimen No. (MVZ):	81354	81359	81360	81356	81357	81358
Sex	Ad. ♀	♀	♀	♂	♂	♂
Weight – gms.	—	2.73	2.95	2.39	2.86	2.86
Total length – mm.	752	199	207	199	213	219
Snout-vent length – mm.	633	168	176	165	174	179
% tail length % total length	15.8	15.6	14.3	17.1	18.3	18.3
Ventrals	217	218	216	195	205	203
Subcaudals	69	67	68	80	84	78
Ventrals & Subcaudals	217	218	216	195	205	203
Umbilical Scar *	—	186	182	170	174	177
Body Bands	28	24	?	22	22	24
Supralabials	8-9	8-8	9-9	8-8	9-8	8-8
Infralabials	13-13	13-12	13-13	11-11	13-12	12-12

* First ventral scale with scar

Five hatchlings have 275-289 ($\bar{x} = 282.8$) total ventral-subcaudal scales. These counts are very similar to counts from other Puebla specimens from the same general area (275-290, $\bar{x} = 284.75$, $N = 8$). The same similarities exist in comparing the total body band counts. Four hatchlings have 22-24 ($\bar{x} = 23.0$) dorsal cross bands while other Puebla specimens have 19-26 ($\bar{x} = 22.3$, $N = 9$) cross bands. The hatchlings also agree with other Puebla specimens of *Trimorphodon* in their supralabial and infralabial counts (Table 2).

EVOLUTIONARY HISTORY

Some brief comments concerning speciation in the genus *Trimorphodon* seem appropriate. Because no fossil remains are known, our interpretation of the evolutionary history of the species is based primarily on an analysis of the distributions and relationships of living forms correlated with the geohistory and paleogeography of the area.

Savage (1966) considered snakes of the genus *Trimorphodon* to be representative of the Middle American Element. Duellman (1958, 1966) suggested that *Trimorphodon* diverged early from the evolutionary stock that gave rise to *Hypsiglena*, *Leptodeira*, *Eridiphas* and *Cryophis*. We concur, and suggest that the ancestor of *Trimorphodon* diverged early in the Cenozoic and probably occupied areas of relatively low relief in northern and central México. Axelrod (1958) has indicated that most of this region was dominated by a Neotropical Tertiary Geoflora. Based on indirect evidence several authors have suggested that a broad ecotone of Arcto-Tertiary Geoflora extended into the mountains of México at this time (Axelrod, 1960; Brame and Wake 1963; Savage, 1966).

As a result of the general cooling trend in the early Tertiary, the northern borders of the tropics began to move towards the equator. In areas of northwestern México and the southwestern United States, elements of a Madro-Tertiary Geoflora, that developed *in situ*, began to spread. The Miocene was a period of major mountain building and general uplift (Maldonado-Koerdell, 1964). The Mexican Plateau, the Sierra Madre Occidental, the Sierra Madre Oriental, and the Sierra Madre del Sur were uplifted to their present height beginning in the Miocene and continuing to the present. This period of orogeny initiated major volcanic action, especially during the Pliocene and Recent, that formed the Transverse Volcanic Range. By the end of Miocene, in response to the gradual Tertiary temperature depression and increasing aridity, much of the tropical vegetation, except the more xeric type, was eliminated from central and western México. In northern México the derivatives of the Madro-Tertiary Geoflora were segregating into their component parts in the late Cenozoic. The mixed coniferous and deciduous derivatives of the Arco-Tertiary Geoflora were found throughout most of the mountainous areas of México.

We suggest that the ancestral *Trimorphodon* stock gave rise to three distinct lineages, each of which was markedly affected by the continuing trends of cooling and aridity and by the late Tertiary period of mountain building and volcanic activity.

The first lineage probably occupied much of central México and gave rise to *Trimorphodon tau*. As the climatic changes continued, this species adapted to dry habitats throughout much of the present Mexican Plateau perhaps as far south as Oaxaca. Tamayo and West (1964) suggested that much of this area, originally drained by the Lerma River included the lake basins drained by the present Río Lerma as far southeast as the Valley of México. With the late Tertiary volcanic activity that gave rise to the Mesa Central (West, 1964) and the Transverse Volcanic Range and the resultant cooler temperatures, this ancestral species was eliminated from the central part of its range and restricted to a horseshoe pattern of distribution north, east and south of the Mesa Central. One segment of this population gave rise to the subspecies *latifascia* in the eastern Balsas Basin. Subsequently, when conditions were suitable, the Balsas population apparently expanded into the Tepalcatepec drainage system and approached the range of the northern segment of the original population. These two ends of the horseshoe are now separated by the western portions of the Transverse Volcanic Range. At the same time that the Balsas-Tepalcatepec populations were expanding, the population ancestral to the subspecies *tau* was expanding northward along the slopes and foothills of the Sierra Madre Occidental and Sierra Madre Oriental.

The second major lineage of *Trimorphodon* evolved in association with the developing Madro-Tertiary Geofloral derivatives and gave rise to the species found in the arid lowlands of the southwestern United States and north-

western México today. We suspect that *Trimorphodon vandenburghi*, *T. lambda* and *T. lyrophanes*, if indeed they are distinct species, were derived from this second major lineage. *Trimorphodon vilkinsonii*, today found in eastern New Mexico, western Texas and adjacent parts of México, likely was derived from the ancestral *lyrophanes* stock and isolated east of the Rocky Mountain-Sierra Madre Occidental mountain system, where it is found today in mountains and foothills on the margin of the Chihuahuan Desert.

The third lineage gave rise to the species *T. biscutatus* and probably evolved in a xeric tropical lowland environment in the Pacific coastal lowlands of southern México and northern Central America. Savage (1966) referred to this species in his discussion of the history of the Western Mesoamerican Complex. *Trimorphodon biscutatus* subsequently dispersed northward along the developing Pacific lowland route as far north as southern Jalisco.

Areas of sympatry or near sympatry between *Trimorphodon biscutatus* and *T. lambda* occur in the southwestern corner of Jalisco. *Trimorphodon tau* is sympatric with *Trimorphodon biscutatus* at Apatzingán, Michoacán and Huajintlán, Morelos and with *Trimorphodon lambda* at Terreros, Sinaloa and about 10 miles west of Alamos, Sonora. Although *T. tau* has been reported from Chihuahua, Chihuahua (Cope 1900) near the type locality of *Trimorphodon vilkinsonii*, this record needs to be verified.

ACKNOWLEDGMENTS

We would like to thank the following people and institutions for allowing us to examine material in their care: Charles M. Bogert and Richard G. Zweifel, American Museum of Natural History, New York (AMNH); Edmond V. Malnate and James E. Bohlke, Academy of Natural Sciences, Philadelphia (ANSP); M. J. Fouquette, Arizona State University, Tempe (ASU); Alice G. C. Grandison, British Museum (Natural History), London (BM); Richard B. Loomis, California State College, Long Beach (CSCLB); Robert F. Inger and Hymen Marx, Field Museum of Natural History, Chicago (FMNH); William E. Duellman, Museum of Natural History, University of Kansas, Lawrence (KU); John W. Wright, Los Angeles County Museum of Natural History, Los Angeles (LACM); Douglas A. Rossman, Louisiana State University, Museum of Zoology (LSUMZ); Ernest E. Williams, Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Walter W. Dalquest, Midwestern University, Wichita Falls, Texas (MU); Robert C. Stebbins, Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); George S. Myers, Museum of Natural History, Stanford University, Palo Alto (SU—collections now housed at California Academy of Sciences, San Francisco); James R. Dixon, Texas Cooperative Wildlife Collection, Texas A & M University, College Station (TCWC); Charles H. Lowe, University of Arizona, Tucson (UAZ); Walter Auffenberg, Florida State Museum, University of Florida, Gainesville (UF); Hobart M. Smith, University of

Illinois Museum of Natural History, Urbana (UIMNH); Charles F. Walker, University of Michigan Museum of Zoology, Ann Arbor (UMMZ); James A. Peters, United States National Museum, Washington, D.C. (USNM); and Günther Peters, Zoologisches Museum Humboldt-Universität, Berlin (ZMB). Robert L. Bezy and C. Jay Cole, and Richard D. Worthington also provided specimens for study. The information on eggs and hatchlings was made available by Joseph L. LaPointe, Ray B. Huey and Ted Papenfuss.

Evie Templeton illustrated the head patterns in Figures 5, 6, and 7. Mercedes McDiarmid and Richard D. Worthington provided technical assistance with the statistical analysis. Allene J. Brown typed the manuscript. David B. Wake and Hymen Marx read the manuscript in final form and made several helpful suggestions. Fred F. Gehlbach kindly relinquished his interest in this group of *Trimorphodon*. Carl L. Hubbs, W. I. Follett and Lillian Dempster offered their advice concerning the proper use of the name *Trimorphodon tau*.

The Society of Sigma Xi provided financial assistance to the first author for field work in Sinaloa in 1962.

To all of these people and institutions we extend our thanks.

SPECIMENS EXAMINED

MÉXICO

Aguascalientes: 7 mi S Rincón de Romos (UIMNH 27566).

Colima: Colima (AMNH 12777); 4.3 mi SW Colima, 575' (UMMZ 114479).

Durango: Ventanas (BM 83.4.16.68 and 69).

Guanajuato: Guanajuato (SU 4412, USNM 11370), Mt. Cubilete (AMNH 93433).

Guerrero: 15 mi NE Acapulco (LACM 7114); Acahuizotla (TCWC 22142); 3 mi WSW Axixintla (UMMZ 126541); Chilpancingo (FMNH 38412-32; KU 24100-03; MCZ 33657-58, 33663-5; UIMNH 34991-93); near Chilpancingo (UMMZ 85769-74); vicinity of Chilpancingo (AMNH 72522-24); 4 mi W Chilpancingo, 5800' (TCWC 9575); 13 m S Chilpancingo, 3750' (KU 67733); 7 mi E Chilpancingo (UIMNH 19139); 40 mi N Chilpancingo (LACM 53026); 25 mi NNE Iguala, 3800' (TCWC 12608); Ojito de Agua, 2.5 mi S Almolonga, 5600' (TCWC 11602-03); Ojito de Agua, 3 mi S Almolonga, 5400' (TCWC 11601); Omilteme, Sierra de Burro Mtns. (MCZ 42677); Palo Blanco, 4800' (TCWC 9574); 15 mi SE Tonatico (UMMZ 126542); Taxco (MCZ 33901).

Hidalgo: 10 km N Jacala (USNM 110401); Zacualtipán (ANSP 14770); 5.6 mi N of road to Zimapán on Hwy 85 (LACM 53023); 5 mi S Zimapán (AMNH 93432).

Jalisco: 2 mi ENE Acatlán, 5300' (KU 67735); 4 mi S Autlán (KU 27191); 2 mi E Bolaños, 3500' (KU 91428); 1 mi NE Contla, 3800' (KU 80762-63); La Cumbre de los Arrastrados, 8500' [Talpa Mascota] (BM 92.10.31.63); Guadalajara (MCZ 46891; USNM 31358-type of *upsilon*); between Hostotipaquillo and Magdalena (AMNH 19582); 10.4 km NNW Ixtlahuacán del Río (KU 102986); Jamay (AMNH

19841); near Magdalena, 1300 m (FMNH 105194); 1 mi NW El Molino, 5100' (AMNH 96652).

México: Ixtapan de la Sal, 5250' (AMNH 71360).

Miahoacán: Apatzingán, 1000' (FMNH 39078-79); 7.6 mi E Apatzingán, 1600' (UMMZ 112514); 14 mi E Apatzingán, 1700' (UMMZ 112516); 17.6 mi E Apatzingán, 1600' (UMMZ 112515); 3.9 mi S Apatzingán (UIMNH 73730); Coalcomán, 945 m (UMMZ 104696-97); 6 mi E Emiliano Zapata, 5350' (UMMZ 118950); 7 mi E Emiliano Zapata, 5400' (UMMZ 118949); 4.3 mi N Lombardía, 2850' (UMMZ 118951); 8.7 mi S Lombardía (UMMZ 124039); Nueva Italia, 1250' (UMMZ 118952); 43 mi S Nueva Italia on Playa Azul Road, 1000' (UAZ 27060); Tacicuaró, 2000 m (FMNH 105193; UIMNH 19138); 5.5 m W Tangamandapio, 5800' (UMMZ 118948); 1.4 mi N Río Tepalcatepec (UIMNH 73729); Tzaráracua Falls, 6 km SE Uruapan (USNM 110400-type of *fasciolata*).

Morelos: Alpuyeca, 3500' (TCWC 4127); 4 mi S Alpuyeca, 3600' (UMMZ 114478); Campo Agrícola, Progreso (UIMNH 26073); camp near Cuernavaca (UIMNH 19135); Huajintlán (UIMNH 19137); km 128, near Puente de Ixtla (FMNH 105100); 12 mi S Puente de Ixtla (UIMNH 19134); Tepoztlán (UIMNH 19136); 6 mi W Yauatepec (TCWC 7390).

Nayarit: Barranquitas (AMNH 75585); 5 mi SE Ixtlán del Río (TCWC 12609); N of San Blas (LACM 53025).

Oaxaca: Juquila Mixes [=Xuquila Mixes] (AMNH 100649); 3 mi NE Mitla, 5800' (AMNH 97985); ca. 2 mi W Mitla, La Fortaleza (AMNH 89629); 17 mi SE Nochistlán, 6900' (TCWC 12640); Oaxaca (FMNH 105305, 105350); 21 mi SE Oaxaca, 5350' (UMMZ 112522); 59 mi NW Ciudad Oaxaca, (UMMZ 121824); Quiotepec (USNM 30338-type of *tau*); San Felipe del Agua, 6500' (AMNH 97988, 100932-33); 2 km W San Felipe del Agua, (UIMNH 60799); Cerro San Felipe (UIMNH 53121, 73654, 74462-64); San Lucas Camotlán (AMNH 89630); 3 mi N San Miguel del Valle, 6950' (AMNH 97986-87).

Puebla: no specific locality (ZMB 6652-syntypes of *latifascia*); 11.4 mi NW Acatlán (LACM 38206); 16 mi N Acatlán (LACM 9509); 6 mi SE Acatlán (KU 31680); 10.1 mi NW Amatlán (UF 11337); 10 mi NW Huajuapán de León on Hwy 190 (MVZ 81355); 26 mi NW Huajuapán de León on Hwy 190 (MVZ 81354); 3 km W Izúcar de Matamoros (KU 39625); 17 mi SE Izúcar de Matamoros (AMNH 89631); San Diego, ca. 5 mi S Tehuacán (USNM 110402-type of *forbesi*); 6.7 mi NNW Tehuizingo (UF 11335); 6.3 mi SE Tehuizingo (UF 11336).

San Luis Potosí: 10.5 mi W Río Verde, 4000' (UMMZ 126193); 2.5 mi S Pendería (LSUMZ 298).

Sinaloa: 16 km NNE Choix, 1700' (KU 68754); 22.1 mi N Culiacán (LACM 53024); 4 mi NNE El Fuerte, 300' (FMNH 71531) 2-3 mi ESE Río Fuerte Dam [8 mi NNE El Fuerte, 300'] (FMNH 71532-33) 8.3 mi N Guacamil [=Guamúchil] (UF 12829); 1.6 mi S Guacamil [=Guamúchil] (UF 12830); Terreros (LACM 9510); near Terreros (LACM 7112); 2.5 mi NW Terreros (LACM 7108); 5 mi NW Terreros (LACM 7109); 7 mi NW Terreros (LACM 7111); 10 mi NW Terreros (LACM 7110); 10.2 mi SE Terreros (LACM 7113).

Sonora: La Aduana, 5 mi W Alamos (LACM 53028); Alamos (AMNH 75119); W

side Alamos (KU 24119); 3.5 mi W Alamos (LACM 9157); 9.7 mi W Alamos, 1300' (LACM 53029); 8 mi SSE Alamos on Río Cuchujaqui, 900' (LACM 53030); Guirocoba (MVZ 50833-34); ca. 15 mi SE Navojoa (MVZ 76372); 18 mi SE Navojoa (MVZ 76373); 20 mi E Navojoa (LACM 53027).

Tamaulipas: 10 km N Antiguo Morelos (MU 196); S Ciudad Victoria, on Hwy 85 between C. Victoria and Llera (UMMZ 111255); 13 mi S Ciudad Victoria (UIMNH 19284); 14 mi S Ciudad Victoria (UIMNH 27164); 23 mi S Ciudad Victoria (AMNH 72399); 24 mi S Ciudad Victoria (AMNH 72400); Gruta de Quintero, near Quintero (AMNH 58224); La Joya de Salas, 1550 m (UMMZ 110882).

Vera Cruz: Jalapa (BM 81.10.31.65); Tuxpango, near Orizaba (USNM 26499-type of *collaris*).

Zacatecas: Hacienda San Juan Capistrano (USNM 46334).

Locality Unknown: "Mexico" (FMNH 42066; USNM 9911-12, 25361, 26138-9 [see Taylor, 1939: 366 for comments]).

"Southern Mexico" (BM 95.1.4.7 A and B)

"Distrito Federal" (AMNH 19718 [see Zweifel, 1959: 7 for comments]).

ADDITIONAL SPECIMENS (*examined but data not included*)

Colima: 4.3 mi SSW Colima, 1300' (UF 24783).

Hidalgo: 10.4 mi NNW Ixmiquilpan, 7500' (UF 27378).

Jalisco: 2 mi NE El Molino (UAZ 27023).

Sonora: 6 mi W Alamos (ASU 6651, 6684); 9 mi W Alamos (ASU 6377); 11 mi W Alamos (ASU 6663, 6712); 14 mi W Alamos (ASU 6648).

LITERATURE RECORDS (*specimens not examined*)

Chihuahua: Batopilas (Cope, 1887: 68; Klauber, 1928: plate 22); city of Chihuahua (Cope, 1900: 1105).

Jalisco: "Jalisco" (Mocquard, 1899: 157); Guadalajara [USNM 12419] (Taylor, 1939: 366; Smith, 1941: 163).

Michoacán: San Salvador [BM 1914.1.28.136] (Peters, 1954: 32-34).

Morelos: between Cuernavaca and Tepoztlán; near Huajintlán (Taylor, 1941: 479).

Nayarit: Sierra del Nayarit (Mocquard, 1899: 157).

Tamaulipas: 14 mi SW Jiménez (Brown and Brown, 1967: 325).

RESUMEN

La variación geográfica en lepidosis y tipo de coloración han sido estudiadas en las siguientes especies nominales *Trimorphodon collaris*, *fasciolata*, *forbesi*, *latifascia*, *tau* y *upsilon*. Los ejemplares fueron agrupados en siete diferentes muestras geográficas que fueron luego comparadas entre sí. La mayoría de las características tienen una amplia distribución y se confunden mas con otras; otras características varían independientemente. Las escamas ventrales y subcaudales disminuyen en número de norte a sur. El número de bandas dorsales en el cuerpo es menor en culebras del Valle de Balsas-

Tepalcatepec, las cuales tienen también coloración uniforme en la cabeza. Ejemplares de otras regiones tienen una compleja coloración cefálica que consiste en bandas prefrontales, bandas interoculares y marcas parietales discretas en varias combinaciones. Estudios de los bandas en el cuerpo y coloración cefálica indican un intercambio genético limitado entre los ejemplares del Valle de Balsas-Tepalcatepec y aquellos de otras regiones, posiblemente como resultado de contacto secundario en el sur de Jalisco y la región adyacente de Michoacán. La Cadena Volcánica Transversa y la Sierra Madre del Sur aparentemente restringen el intercambio genético.

Estas especies nominales se asignan al sinónimo *Trimorphodon tau*. El nombre *Trimorphodon tau tau* se conserva para las poblaciones de las colinas y la meseta y *T. tau latifascia* (nueva combinación) se asigna a la población del Valle de Balsas-Tepalcatepec. *Trimorphodon tau* es redescribo y se delimita su distribución. La variación en características de un grupo procedente de Puebla es semejante a la variación típica que se encuentra en la muestra total de Puebla.

LITERATURE CITED

- DO AMARAL, A. 1929. Estudos sobre ophidios neotropicos. XVIII. Lista remissiva dos ophidios da regioao neotropicos. Inst. Butantan, Mem., 4: 129-271.
- AXELROD, D. I. 1958. Evolution of the Madro-Tertiary Geoflora. Bot. Review, 24(7): 433-509.
- . 1960. The evolution of flowering plants. In Tax, S (ed.), Evolution after Darwin. Chicago, Univ. Chicago Press, Vol. 1, The Evolution of life: 227-305.
- BOULENGER, G. A. 1896. Catalogue of the Snakes in the British Museum (Natural History). London, vol. 3, 727 p., 25 plates.
- BRAME, A. H., AND D. B. WAKE. 1963. The salamanders of South America. Los Angeles County Mus., Contrib. Sci., 69: 1-72.
- BROWN, B. C. AND L. M. BROWN. 1967. Notable records of Tamaulipan snakes. Texas J. Sci., 29(3): 323-26.
- COPE, E. D. 1869. Seventh contribution to the herpetology of tropical America. Amer. Phil. Soc., Proc., 11: 147-170, figs. 9-11.
- . 1875. On the Batrachia and Reptilia of Costa Rica. Acad. Natur. Sci., Philadelphia, J., ser. 2, 8(4): 93-154.
- . 1886. Thirteenth contribution to the herpetology of tropical America. Amer. Phil. Soc., Proc., 23: 271-287.
- . 1887. Catalogue of the batrachians and reptiles of Central America and México. U.S. Natl. Mus., Bull., 32: 1-98.
- . 1892. A critical review of the characters and variations of the snakes of North America. U.S. Natl. Mus., Proc., 14(882): 589-694.
- . 1900. The crocodilians, lizards, and snakes of North America. U.S. Natl. Mus., Rep., 1898: 153-1270, figs. 1-347, plates 1-36.
- DAVIS, W. B. AND H. M. SMITH. 1953. Snakes of the Mexican state of Morelos. Herpetologica, 8(4): 133-149.
- DAVIS, W. B. AND J. R. DIXON. 1957. Notes on Mexican snakes (Ophidia). South-western Natur., 2(1): 19-27.

- . 1959. Snakes of the Chilpancingo Region, México. Biol. Soc. Washington, Proc., 72: 79-92.
- DOWLING, H. G. 1951. A proposed standard system of counting ventrals in snakes. British J. Herpetol., 1(5): 97-99.
- DUELLMAN, W. E. 1958. A monographic study of the colubrid snake genus *Leptodeira*. Amer. Mus. Natur. Hist., Bull., 114(1): 1-152. 31 plates.
- . 1958. A preliminary analysis of the herpetofauna of Colima, México. Mus. Zool. Univ. Michigan, Occ. Papers, 589: 1-22.
- . 1961. The amphibians and reptiles of Michoacán, México. Univ. Kansas Publ. Mus. Natur. Hist., 15(1): 1-148.
- . 1965. A biogeographic account of the herpetofauna of Michoacán, México. Univ. Kansas Publ. Mus. Natur. Hist., 15(14): 627-709.
- . 1966. Remarks on the systematic status of certain mexican snakes of the genus *Leptodeira*. Herpetologica, 22(2): 97-106.
- DUMERIL, A. M. C., G. BIBRON AND A. DUMÉRIL. 1854. Erpétologie generale au histoire naturelle complete des reptiles. Paris, 7, 2nd part: 782-1536.
- EBERHARDT, L. L. 1968. An approximation to a multiple-comparison test. Copeia, 1968(2): 314-319.
- FOUQUETTE, M. J., JR. AND D. A. ROSSMAN. 1963. Noteworthy records of Mexican amphibians and reptiles in the Florida State Museum and the Texas Natural History Collection. Herpetologica, 19(3): 185-201.
- FOX, W. 1948. Effect of temperature on development of scutellation in the garter snake, *Thamnophis elegans atratus*. Copeia, 1948(4): 252-262.
- GADOW, H. 1905. The distribution of Mexican amphibians and reptiles. Zool. Soc. London, Proc., 1905(2): 191-244.
- . 1910. The effect of altitude upon the distribution of Mexican amphibians and reptiles. Zool. Jahrbuch, 29(6): 689-714.
- GARMAN, S. 1883. The reptiles and batrachians of North America. Mus. Comp. Zool. Harvard Univ., Mem., 8(3): 1-185, plates 1-9.
- GÜNTHER, A. C. L. G. 1895. Biologia Centrali-Americana. Reptilia and Batrachia. 1885-1902. London, i-xx, 326 p., 76 plates.
- HALL, C. W. 1951. Notes on a small herpetological collection from Guerrero. Univ. Kansas Sci. Bull., 34 (pt. 1), (4): 201-212.
- HARDY, L. M. AND R. W. MCDIARMID. 1969. The amphibians and reptiles of Sinaloa, México. Univ. Kansas Publ. Mus. Natur. Hist., 18(3): 39-252.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1964. International code of zoological nomenclature. London, 176 p.
- JAN, G. 1863. Elenco sistematico degli ofidi descritti e disegnati per l'Iconografia generale. Milano, 143 p.
- JAN, G. AND F. SORDELLI. 1872. Iconographia générale des ophidiens. Milan, vol. 3, livr. 39, plate 1, fig. 3.
- JONES, C. AND J. S. FINDLEY. 1963. Second record of the lyre snake *Trimorphodon vilkinsonii* in New Mexico. Southwestern Natur., 8(3): 175-177.
- KLAUBER, L. M. 1928. The *Trimorphodon* (lyre snake) of California, with notes on the species of the adjacent areas. San Diego Soc. Nat. Hist., Trans., 5(11): 183-194, 2 plates.
- . 1941. The correlation between scalation and life zones in San Diego County snakes. Zool. Soc. San Diego, Bull., 17(3): 73-79.

- . 1956. Rattlesnakes. Their habits, life histories and influence on mankind. 2 vols., Univ. California Press, Berkeley and Los Angeles, 1476 p.
- LEOPOLD, A. S. 1950. Vegetation zones of México. *Ecology*, 31(4): 507-518.
- LYNCH, J. D. AND H. M. SMITH. 1965. New or unusual amphibians and reptiles from Oaxaca, México. I. *Herpetologica*, 21(3): 168-177.
- MALDONADO-KOERDELL, M. 1964. Geohistory and paleogeography of Middle America. In Wauchope, R. (ed.), *Handbook of Middle American Indians*. Univ. Texas Press, Austin, Vol. I, Natural environment and early cultures, Chapt. 1: 3-32.
- MARTIN, P. S. 1958. A biogeography of reptiles and amphibians in the Gomez Farias Region, Tamaulipas, México. *Mus. Zool. Univ. Michigan, Misc. Publ.*, 101: 1-102, 7 plates.
- MOCQUARD, M. F. 1899. Reptiles and batraciens recueillis au Mexique par M. Léon Diquet en 1896 et 1897. *Soc. Philom. Paris, Bull.*, 9 ser., 1(4): 154-169, 1 plate.
- . 1908. In Duméril, A. and M. Bocourt. *Études sur les Reptiles. Recherches Zoologiques pour servir à l'histoire de la faune de l'Amérique Centrale et du Mexique*. Mission Scientifique au Mexique et dans l'Amérique Centrale. Paris, vol. 3, i-xiv, 1012 p., 77 plates.
- PETERS, J. A. 1954. The amphibians and reptiles of the coast and coastal Sierra of Michoacán, México. *Mus. Zool. Univ. Michigan, Occ. Papers*, 554: 1-37.
- PETERS, W. C. H. 1869. Über mexicanische Amphibien, welche Hr. Berkenbusch in Puebla auf Veranlassung des Hrn. Legationsraths von Schlozer dem zoologischen Museum zugesandt hat. *Akad. Wiss. Berlin, Monatsber.*, 1869: 874-881.
- SAVAGE, J. M. 1966. The origins and history of the Central American herpetofauna. *Copeia*, 1966(4): 719-766.
- SCHMIDT, K. P. AND F. A. SHANNON. 1947. Notes on amphibians and reptiles of Michoacán, México. *Chicago Natur. Hist. Mus., Fieldiana Zool.*, 31(9): 63-85.
- SMITH, H. M. 1941. Notes on the snake genus *Trimorphodon*. *U.S. Natl. Mus., Proc.*, 91(3130): 149-168.
- . 1943. Summary of the collections of snakes and crocodilians made in México under the Walter Rathbone Bacon Traveling Scholarship. *U.S. Natl. Mus., Proc.*, 93(3169): 393-504.
- SMITH, H. M. AND E. H. TAYLOR. 1945. An annotated checklist and key to the snakes of México. *U.S. Natl. Mus., Bull.*, 187: 1-239.
- SMITH, P. W. AND D. M. DARLING. 1952. Results of a herpetological collection from eastern central México. *Herpetologica*, 8(3): 81-86.
- STEBBINS, R. C. 1949. Speciation in salamanders of the plethodontid genus *Ensatina*. *Univ. California Publ. Zool.*, 48(6): 377-526.
- SUMICHRIST, F. 1882. Enumeracion de las especies de reptiles observados en la parte meridional de la República Mexicana. *La Naturaleza*, 6(2): 31-45.
- TAMAYO, J. L. AND R. C. WEST. 1964. The hydrography of Middle America. In Wauchope, R. (ed.) *Handbook of Middle American Indians*. Univ. Texas Press, Austin. Vol. I, Natural environment and early cultures, Chapt. 3: 84-121.
- TAYLOR, E. H. 1939. On Mexican snakes of the genera *Trimorphodon* and *Hypsiglena*. *Univ. Kansas Sci. Bull.*, 25(16): 357-383, plates 35-38 (1938).
- . 1940. Some Mexican serpents. *Univ. Kansas Sci. Bull.* 26(14): 445-487, plates 49-52 (1939).
- . 1949. A preliminary account of the herpetology of the state of San Luis Potosí, México. *Univ. Kansas Sci. Bull.*, 33, pt. 1, (2): 169-215.

- VIVO ESCOTO, J. 1964. Weather and climate of México and Central America. *In* Wauchope, R. (ed.) Handbook of Middle American Indians. Univ. Texas Press, Austin, Vol. 1, Natural environment and early cultures, Chapt. 6: 187-215.
- WEBB, R. G. AND C. M. FUGLER. 1957. Selected comments on amphibians and reptiles from the Mexican state of Puebla. *Herpetologica*, 13(1): 33-36.
- WEST, R. C. 1964. Surface configuration and associated geology of Middle America. *In* Wauchope, R. (ed.) Handbook of Middle American Indians. Univ. Texas Press., Austin. Vol. 1, Natural environment and early cultures, Chapt. 2: 33-83.
- ZWEIFEL, R. G. AND K. S. NORRIS. 1955. Contribution to the herpetology of Sonora, Mexico: description of new subspecies of snakes (*Micruroides euryxanthus* and *Lampropeltis getulus*) and miscellaneous collecting notes. *Amer. Midland Natur.*, 54(1): 230-249.
- ZWEIFEL, R. G. 1959. The provenance of reptiles and amphibians collected in western México by J. J. Major. *Amer. Mus. Natur. Hist.*, Novitates 1949: 1-9.
- . 1959. Additions to the herpetofauna of Nayarit, México. *Amer. Mus. Natur. Hist.*, Novitates, 1953: 1-13.
- . 1961. Another method of incubating reptile eggs. *Copeia*, 1961(1): 112-113.

Accepted for publication June 30, 1969.